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Response of a peatland ecosystem to stratospheric ozone reduction in Tierra del Fuego

Thomas Matthew Robson
Utah State University

RESPONSE OF A PEATLAND ECOSYSTEM TO STRATOSPHERIC OZONE REDUCTION IN TIERRA DEL FUEGO

by

Thomas Matthew Robson

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ABSTRACT

Response of a peatland ecosystem to stratospheric ozone

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by

Thomas Matthew Robson, Doctor of Philosophy

Utah State University, 2004

Major Professor: Dr. Martyn M. Caldwell
Department: Forest, Range, and Wildlife Sciences

Tierra del Fuego, at the southernmost tip of South America, is influenced by ozone depletion. The landscape of southern and western Tierra del Fuego is dominated by peatlands; they are important locally and in the context of global climate change, because they store large quantities of organic carbon.

To determine the influence of solar ultraviolet-B radiation (UV-B) on a Tierra del Fuego peatland, we selectively filtered solar UV-B in ten pairs of plots. Polyfluorine filters were used to create the Near-Ambient-UV-B Treatment (90% solar UV-B), and polyester filters to create the Reduced-UV-B Treatment (17% solar UV-B). These filters were first installed in October 1996, and were maintained, September-March, for six years. Following previous plant growth measurements and samples of selected microorganisms under the two UV-B treatments (1996-1999), this dissertation is an account of the more detailed measurements made during the second three-year period of

treatments (1999-2001). Seasonal sampling of the plant community, microfungi, microfauna, and biogeochemistry of the water and nutrients held by the *Sphagnum* capitulum was introduced, in an attempt to better understand ecosystem function.

Solar UV-B reduced *Sphagnum* height growth, but this was compensated by more compressed and densely packed *Sphagnum* capitula. Emergent vascular plants, *Nothofagus*, *Empetrum*, and *Tetroncium,* were more affected than *Sphagnum* by near-ambient UV-B. Solar UV-B altered the *Sphagnum*-capitulum microenvironment, resulting in: more dissolved organic carbon and phosphorous, higher electrical conductivity, and greater acidity under near-ambient UV-B. Additionally, the populations of testate amoebae and some species of fungi were consistently increased; however, microfungal diversity and rotifer, nematode, and mite populations decreased under near-ambient UV-B.

Generally, *Sphagnum* minimizes the leaching of nutrients by effectively holding water at the capitulum. Solar UV-B altered *Sphagnum*-capitulum morphology, increased the volume of water held, and made this water more acidic and richer in nutrients. Based on these results, if current trends in ozone depletion were to persist over several decades, a reduction in vascular plant growth, and changes in the trophic relationships of the microorganismal community of the *Sphagnum* capitulum, would be predicted. These responses have the potential to affect peatland carbon storage and nutrient cycling in Tierra del Fuego.

(159 pages)

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T. M. Robson

FOREWORD

My first trip to Tierra del Fuego was in February of 1999. It is quite a tour to travel from Utah to Ushuaia through Chicago and Buenos Aires in February, through so many of the world's climates. Descending at dusk in early spring after a recent snow fall, Ushuaia looked a very alluring place. The land captured in shades of contrasting white and grey shadows, nothing more, with a slate grey sea and sky. I was invigorated by the fresh air blown in from Antarctica and the southern oceans and captivated by the almost-daily rainbows and long spectacular sunsets against panoramic vistas. Indeed, the high profile enjoyed by the ever-changing weather of Tierra del Fuego gave the impression of a location most fitting to be considering life under the sun!

This preparatory visit in February of 1999 allowed me to see the experimental set-up, established since 1996, and to meet the research team in Ushuaia. During the following 1999-2000 season, with the transition from the original researchers complete, I took charge of the peatland site. The old boardwalk use to access the plots required considerable maintenance and was raised to escape the engulfing *Sphagnum*. Also, field sites for investigation of the three *Nothofagus* species were selected, and branch filter designed and installed. These sites were maintained for a further three years and produced much useful data. Also, at the end of the field season, 1999-2000, tree-ring cores were taken from 50 *Nothofagus* trees in the National Park, and sent to Buenos Aires for analysis. The highlight of my first term in Ushuaia was the unprecedented end of millennium festivities that saw global media attention at "The Edge of the World".

The austral spring of 2000-2001 was miserably wet. Even escape to the northern beach-resort of Mar del Plata in November for an international UV-conference brought

no respite from the rain! Though our old Ford project van finally gave out on us, the group was undeterred by the torrents, managing to run an herbivory study using the "little wizards of the forest". The group also entertained by a photographer from the New York Times following us around to two weeks.

Political and economic chaos hit Argentina during our 2001-2002 field season. We quickly needed to master the local banking and bartering systems to keep the project running smoothly. In probably my most fruitful period of research, I concluded the long-term measurements and sampling, and managed to successfully collaborating with Verónica Pancotto, my counterpart in Buenos Aires, to publish an interesting decomposition study.

My final visit to Tierra del Fuego in February of 2003, gave me the opportunity to test a prototype system for determining the effect of UV-B on fungal cultures from the peatland, giving me the data to put the final touches to the third chapter of this dissertation. I had the chance to develop some novel ideas for using *Tetroncium* rhizomes in peatland research. And of course, having been spoilt by my experience of seven consecutive summers, my acclimation to the Utah winter was softened!

T. M. Robson

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CHAPTER 1

INTRODUCTION

A general erosion of the stratospheric ozone layer leading to an annual Antarctic ozone hole has occurred since the 1970's (Molina & Rowland, 1974). Ozone depletion is known to be caused by man-made chemicals (largely halogenated fluoro-carbons), whose production has been restricted since the 1987 Montreal Protocol. The ozone layer is expected to recover; however; the rate of recovery is difficult to predict with confidence because of interactions with other global climate changes and human activities (Solomon, 2004). Meanwhile, there has been little indication that recovery has started, since some of the most severe ozone depletion has occurred during four of the last five austral springs (1999-2004). It is worthwhile to investigate the effects of solar UV-B on those ecosystems that receive increased UV-B as a result of ozone depletion whilst an annual ozone hole continues to form and uncertainties remain as to the longevity of this phenomenon.

Tierra del Fuego, as the southern-most landmass outside Antarctica, is susceptible to the effects of ozone depletion. Every year during the austral spring, southern South America receives an increased dose of UV-B radiation due to ozone depletion. This results from both: a general erosion of the ozone layer over Tierra del Fuego, regularly allowing increased UV-B radiation to pass to the Earth's surface; and direct passage of the ozone hole overhead for a few days each year, leading to a sharp increase in UV-B received relative to the normal daily UV-B dose (Appendix A & Rousseaux *et al.*, 1999). Nevertheless, the total UV-B received by Tierra del Fuego remains low compared with

that at lower latitudes (Díaz *et al.*, 2001). Low solar angles, inclement weather, and greater stratospheric thickness, all reduce the UV-B flux received at high latitudes.

Studies of the effects of UV-B in Tierra del Fuego are interesting because, although total flux is low, UV-B received is substantially higher than pre-depletion doses. The organisms of Tierra del Fuego are adapted to a low UV-B environment, and there is evidence that their defence mechanisms may not be as well developed as those of organisms at lower latitudes (Giordano *et al.*, 2003). Additionally, a number of small responses to UV-B at an organismal level may be propagated into more substantial effects when multiplied to an ecosystem level. Subtle effects of UV-B in the ecosystems of Tierra del Fuego at an organismal level were revealed by the first three years of UV-B manipulations (Searles, 2000). To assess the true importance of these effects in the context of ozone depletion, it is important to know whether these changes diminish, persist, or are cumulative, over a longer period of time. With this in mind, it was decided to continue investigation into UV-B effects on the ecosystems of Tierra del Fuego for at least a further three years.

Peatlands dominate the south and west of Tierra del Fuego. They provide a good opportunity to study the influence of UV-B, because they are finely balanced ecosystems, in which subtle responses to small environmental perturbations may substantially change them (Weltzin *et al.*, 2003). Given the importance of peatlands in global carbon storage, combined with their prevalence at high latitudes (particularly in the Northern Hemisphere), any changes effected by UV-B in our experiments could feedback to have potentially significant wider repercussions for climate change in general. For example,

changes in the flora or rate of decomposition due to UV-B would alter peatland carbon storage.

One disadvantage of studying peatlands at high latitudes is that slow growth and a short growing season mean that any treatment effects are likely to be slow to emerge. Given this, I decided to continue to research the aspects of peatland ecology investigated by Peter Searles (2000) during the first three years of this project. He reported that influences of UV-B on a Tierra del Fuego peatland were subtle, and in some cases high spatial variability of response made it unclear whether or not UV-B had an effect on those organisms studied. I aimed to tease out effects of UV-B, by scaling up from the study of organisms, to population and community levels; and conversely, by breaking groups of organisms into individual species, to isolate species specific responses to UV-B. The scope of the investigation was increased by expanding the range of measurements and frequency of sampling. Measurements over the duration of each field season tested whether temporal variation in solar UV-B was correlated with the occurrence of a treatment effect. The population of micro-organisms and the timing of plant growth and development were monitored to better understand the dynamics of the ecosystem.

I studied the influence of UV-B on each of the four most important components of the peatland ecosystem. This was achieved by the use of two special plastic-film filters to create two UV-B treatments: A near-ambient UV-B treatment of *c* 90% of solar UV-B and a reduced UV-B treatment of c 17% of solar UV-B. These contrast with an estimated increase of *c* 20% in annual solar UV-B received in Tierra del Fuego, compared to pre-depletion values (Searles, 2000). In the plant community (Chapter 2), I investigated

whether the relationship between *Sphagnum* and the emergent vascular plants in the peatland was affected by UV-B. The slow growth rates in this peatland mean that a greater reduction in growth of vascular plants than of *Sphagnum* of just a few cm per year would enable *Sphagnum* to completely engulf the peatland vascular plants within a few field seasons.

Peatland fungi (Chapter 3) provide a readily measurable indication of the conditions at the surface of the peatland, and enact the first stages of *Sphagnum* decomposition. Rather than a generic effect on fungi, specific fungal species are frequently reported to respond singly to UV-B (Newsham *et al.*, 1997; Moody *et al.* 1999, 2001). By isolating these species-specific responses I hoped to reveal something about the mechanism of action of UV-B: For example: 1) do pigmented and non-pigmented fungi respond differently to UV-B; 2) are UV-B effects more pronounced at higher trophic levels in the food web, and does this have a top-down influence? Fungi and bacteria constitute the base of the peatland food web, and as such changes in the fungal community can feedback to influence organisms at higher trophic levels. One such group of organisms are the testate amoebae.

Testate amoebae (Chapter 4) are particularly sensitive to changes in biogeochemical cycling and plant competition in peatlands, and have been used as early indicators of environmental perturbations (Mitchell *et al.*, 2000). Complex relationships occur among the microfaunal community, which could lead to a stronger UV-B effect higher in the food web. In an attempt to understand how plants, fungi and the peatland microfauna interact, new measurements of pH, ionic conductivity, dissolved nitrogen, phosphorus, and carbon were made during the sixth field season of treatments (Chapter 4).

Synthesizing the data from four key aspects of peatland ecology; plants (Chapter 2); fungi (Chapter 3); mirofauna (Chapter 4); and biogeochemistry (Chapters 3 & 4), I endeavor to construct a comprehensive picture of how solar UV-B affects a Tierra del Fuego peatland.

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CHAPTER 2

SIX YEARS OF SOLAR UV-B MANIPULATIONS AFFECT GROWTH OF *SPHAGNUM* AND VASCULAR PLANTS IN A TIERRA DEL FUEGO PEATLAND[1]

Abstract

- Tierra del Fuego is subject to increases in solar UV-B radiation in the austral spring and summer due to ozone depletion.
- Plastic films were used to filter solar UV-B radiation over peatland plots through six field seasons, resulting in near-ambient (*c* 90%) and reduced (*c* 17%) solar UV-B treatments.
- As in the first three field seasons of treatments, near-ambient UV-B caused reduced height growth but had no effect on biomass production of the moss *Sphagnum magellanicum.* It reduced leaf and rhizome growth of *Tetroncium magellanicum.* Height growth and morphology of *Empetrum rubrum* and *Nothofagus antarctica* were only affected by solar UV-B during the fourth through sixth field seasons. There was also a decrease in *Tetroncium* leaf nitrogen under near-ambient UV-B.
- Growth of *Sphagnum* was less affected than that of most emergent vascular plants. This enabled the *Sphagnum* mat to engulf more *Nothofagus,* and limit the escape of *Empetrum* under near-ambient UV-B. Yet, differences in the response of species to solar UV-B were not expressed as changes in plant community composition.

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[1] Co-authored by TM Robson, VA Pancotto, SD Flint, CL Ballaré, OE Sala, AL Scopel & MM Caldwell. *New Phytologist* (2003) **160**: 379-389. The New Phytologist Trust & Blackwell Scientific Publishing.

Introduction

A stratospheric "ozone hole" has formed above Antarctica during the austral spring (September - November) every year since the late 1970's (Farman *et al.,* 1985). This depletion of the ozone layer often extends beyond Antarctica to Tierra del Fuego along with the associated increased ultraviolet-B radiation (UV-B) (Frederick *et al.,* 1994; Díaz *et al.,* 2000).

In Antarctica, solar UV-B was shown to reduce the rate of vegetative growth and leaf expansion of a native grass, *Deschampsia antarctica* Desv., and a forb, *Colobanthus quitensis* (Kunth) Bartl., compared with plants under filters that blocked much of the UV-B (Ruhland & Day, 2000; Day *et al.*, 2001; Xiong *et al.*, 2002). In short experiments with mosses, solar UV radiation had no effect on *Bryum argenteum* Hedw. (Green *et al.,* 2000) and *Sanionia uncinata* (Hedw.) Loeske (Montiel *et al.*, 1999; Lud *et al.,* 2003). However, significant changes in pigmentation due to short-term UV-B fluctuations have been detected in Antarctic mosses (Newsham *et al.,* 2002).

Tierra del Fuego, situated at the most southerly tip of South America, experiences the greatest increase in UV-B radiation as a consequence of ozone depletion of any region outside Antarctica (Díaz *et al.,* 1996; Cede *et al.*, 2002). This is most pronounced during October, when the "ozone hole" can sometimes pass directly over Tierra del Fuego. Consequently, short-term increases in UV-B radiation of up to 50% from day to day can occur at Ushuaia, Argentina (55°S) (Díaz *et al.,* 2001). Also, the subsequent break-up of the Antarctic vortex (November - early December) allows pockets of ozone-depleted air to pass over this region later in the growing season.

High latitudes have historically received little UV-B radiation (Caldwell *et al.*, 1980). Thus, current decreases in the thickness of the ozone layer cause large relative increases in UV-B flux, although compared to lower latitudes, especially the tropics, total UV-B flux remains small. Since organisms have evolved under low background UV-B flux, they may be sensitive to a large relative increase in UV-B radiation. The location of Tierra del Fuego presents an opportunity to study more diverse plant communities than occur in Antarctica and yet still experience the effects of increased solar UV-B radiation (Díaz *et al.*, 2000, 2001).

Interspersed among mature *Nothofagus* forest stands, along stream and lake margins, peatlands form an important component of the landscape of southern Tierra del Fuego (Roig, 2000). The composition of the Tierra del Fuego peatlands is comparable to those of the Northern Hemisphere; *Sphagnum magellanicum* is a widespread peatland species (Daniels & Eddy, 1985), whilst *Empetrum rubrum* is a dominant vascular plant, similar to *Empetrum hermaphroditum* in the Northern Hemisphere.

The overall objective of the investigation was to follow changes in the peatland plant community through six years of solar UV-B manipulation. This paper concentrates on the last three years. After the first three years of UV-B manipulation in this peatland, Searles *et al.* (1999, 2002), observed a small reduction in *Sphagnum* height growth (*c* 15%), and a decrease in size of the largest leaf of *Tetroncium* (*c* 14% in November), but no growth responses of *Empetrum* or *Nothofagus* to the solar UV-B manipulations. Based on these findings, we continued with another three years of more intensive investigation into plant responses to solar UV-B treatments. We aimed to assess whether longer-term UV-B treatments would result in more conspicuous responses of the

Sphagnum and emergent vascular plants to solar UV-B manipulations. Furthermore, we examined whether changes in growth and morphology of *Sphagnum* and the vascular plant species would be evident as shifts in species composition and density within the plant community.

Materials and Methods

The study site is a peatland of approximately 1500 × 500 m. It is located in Tierra del Fuego National Park (54°51'S 68°36'W) to the north of a small lake (Laguna Negra) and stream, otherwise surrounded by mature *Nothofagus* forest. The peatland derives all its water from precipitation, and has a pH of 4.5-6.5. The ground water level drops to *c* 40-cm depth when the peatland is driest in late summer. This peatland was chosen because it has a relatively high plant diversity, homogeneously distributed over its area.

The peatland receives 500-600 mm precipitation annually. Precipitation over the five-month growing season (October - February) was approximately 260 mm (1999-2000), 312 mm (2000-2001) and 269 mm (2001-2002) (T M Robson, unpublished data). The mean annual temperature is 5-6.5° C, reflecting the oceanic climate.

The peatlands of Tierra del Fuego have been well characterized by Mark *et al.* (1995), and Roig (2000). *Sphagnum magellanicum* (Brid.) forms an almost continuous mat, with occasional hummocks and small pools bordered by *Sphagnum fimbriatum* Wils. Of the emergent vascular plants, *Nothofagus antarctica* (Forster f.) Oersted *(Nothofagaceae)* (southern beech) is most abundant along the forest border. This species usually grows as a small tree, but is severely stunted in the peatland, typically reaching only a few cm above the *Sphagnum* mat. *Empetrum rubrum* Vahl ex Willd *(Empetraceae)* (crowberry)

is a creeping evergreen woody perennial, which dominates on the drier tops and sides of the hummocks; *Tetroncium magellanicum* Willd *(Juncaginaceae)* (arrow-rush) grows in the wetter hollows and depressions between hummocks. In addition, *Nanodea muscosa* Banks ex C.F.Garertner, a hemiparasite of *Sphagnum* peatlands, *Juncus scheuchzerioides* Gavdich, and *Pernettya pumila* (c.f.) Hooker are found at lower density throughout the site (Moore, 1983). Most of the vascular plant species are visible as ramets emerging from the *Sphagnum* mat. Nearby ramets are often part of the same genet divided beneath the peatland surface.

Treatment plots

Ten pairs of 1.4 × 2-m experimental plots were selected during October of 1996 in level and homogeneous areas of the *Sphagnum* mat (Searles *et al.,* 1999). Near-ambient and reduced UV-B treatments were randomly assigned within the pairs of plots. Plastic-film filters were suspended horizontally from frames (*c* 40 cm) above the plots to create the UV-B treatments (see photo, Ballaré *et al.,* 2001). A uniform pattern of slits was melted into the filters producing a matrix of small louvers (2 × 25 mm) distributed over the entire filter that enabled water from precipitation to penetrate evenly to the *Sphagnum* mat. Also, we did not wish to totally exclude UV-B in the reduced UV-B treatment. The reduced UV-B treatment was achieved using perforated polyester filters (100-μm thick, optically equivalent to "Mylar-D", Dupont Co., Wilmington, Delaware, USA) that attenuate *c* 83% of the short wavelength UV-B radiation and transmit most of the UV-A radiation (Searles *et al.,* 2002). Near-ambient UV-B plots were covered by perforated polyfluorine filters ("Aclar" type 22A, 38-μm thick, Honeywell, Pottsville, Pennsylvania,

USA) that block *c* 10% of the UV-B (see Searles *et al.,* 2002; Zaller *et al.*, 2002, for more details).

The precipitation passing through the two filter types was found to be approximately equal. Photosythetically active radiation (PAR – total quantum flux in the 400-700 nm waveband) was measured with a quantum sensor (LiCor, Lincoln, Nebraska, USA) at the study site in Tierra del Fuego National Park. This showed that 83-95% PAR radiation was transmitted through both filter types (data not shown).

Filters were installed in late September to coincide with snow melt in the peatland, and remained in place until late March in each of the three field seasons (1999-2002), following the same protocol as Searles *et al.* (1999, 2002). Broken filters were replaced within a day, and a complete replacement of filters was made after three months, in late December. Filter attenuation remained unchanged over this time period (Searles *et al.*, 2002).

For the duration of the experiment, under both of the UV-B treatments, air, surface and below-surface temperatures, precipitation, and UV-B radiation were monitored (21x datalogger, Campbell Scientific, Logan, Utah, USA) and compared with ambient values (Appendix A).

Growth measurements

Growth measurements were continued on *Sphagnum, Empetrum*, *Tetroncium,* and *Nothofagus*, the same plant species studied during the first three years of the experiment (Searles *et al.,* 2002). For continuity and comparability, growth was measured in the same way as during the first three years of the project. Because *Sphagnum* peatlands are

known to exhibit considerable inherent microsite variability (Gerdol, 1996; Mitchell *et al.*, 2000; Phoenix *et al.*, 2003), and responses to UV-B in the first three years of this project were subtle (Ballaré *et al.*, 2001; Searles *et al.*, 2002), we increased the sample size to include 12 ramets of each species per plot.

Sphagnum growth

Ten new color-coded cranked wires (Clymo, 1970) were inserted into each plot in February of 1999 to allow time for the *Sphagnum* to recover from any associated disturbance (Searles *et al.*, 2002) before the first measurements in September, 1999. The vertical growth of the *Sphagnum* mat up these wires (and two existing wires) was measured four times through each growing season to determine seasonal growth patterns. Existing wires were used to compare height growth of *Sphagnum* under the filters and in the open, to determine the influence of the plot microclimate on growth during the fourth and fifth field seasons. These measurements showed that *Sphagnum* height growth was greater under the near-ambient UV-B filter than in the open (data not shown).

At the beginning and end of the sixth field season, *Sphagnum* capitulum density was measured non-destructively. The number of *Sphagnum* capitula in a 120 × 120-mm area was counted, and six randomly assigned counts per plot were taken. *Sphagnum* capitulum mass was sampled at the same time that density was censused and height growth was measured.

Annual *Sphagnum* biomass production and volumetric density of capitula were calculated from height growth, density, and biomass data. To calculate biomass increase per stem, a capitulum correction factor was used following Gehrke (1998). A random

sample of 14 *Sphagnum* capitula were removed from each plot and cut into two 5-mm lengths, 0-5 mm and 5-10 mm from the apex (for calculation of the capitulum correction factor). Samples were oven dried at 65°C at least 72 hours and subsequently weighed to obtain dry mass.

Tetroncium measurements

Tetroncium leaf length (second to fifth leaves produced), and total number of green and senescent leaves were measured during November, December, and towards the end of the growing season every year. In March of 2002, 12 ramets per plot were harvested for measurement of rhizome growth. *Tetroncium* grows sympodially from a rhizome, branching from the leaf axil. Each leaf produced leaves a scar around the rhizome's circumference, which persists for several decades, allowing retrospective growth measurements to be taken. Tightly packed leaf scars correspond to late season growth, allowing annual rhizome growth to be determined as in other rhizomous plants (Duarte *et al.*, 1994; Moen & Walton, 1996). Total rhizome elongation over each of the last seven years was measured, as was the distance between each of the most recent 13 leaf scars, to reveal the seasonal pattern of elongation over the year. Frequencies of rhizome division and root production from the rhizome were counted at the same time as the leaf scars.

Twelve leaves per plot were harvested in February of 2001, air dried, pooled, ground, and sealed in aluminum foil for analysis of their carbon and nitrogen composition. This analysis was carried out at Utah State University Analytical Laboratories, using a CHN1000 analyzer (LECO corporation, St Joseph, Michigan, USA).

Empetrum measurements

Annual stem elongation of *Empetrum* was measured as distance from an annual terminal bud scar on the stem to the shoot apex (Searles *et al.,* 1999, 2002). Growth measurements of the same plants were taken once every field season in March, as was distance from the shoot apex to the *Sphagnum* mat. These plants had three to four years of growth above the *Sphagnum* mat when first selected in September of 1999.

Annual terminal bud scars were used to carry out a retrospective analysis of *Empetrum* growth. Twelve ramets of various sizes were harvested from each plot every field season for more detailed measurements of the number of leaves, branching frequency, and total annual stem and branch growth (up to seven branches) following Shevtsova *et al.* (1997). A comparison was made between the last three field seasons (1999-2002), and the first three field seasons (1996-1999; ramets harvested in February of 2000). The harvest of a range of ramets allowed the treatment effects on ramets differing in their years of growth above the *Sphagnum* mat to be assessed independently.

Nothofagus measurements

Nothofagus ramets with at least three years of stem growth visible above the *Sphagnum* mat were selected in September, 1999. Stem length and leaf production were measured twice during each field season. Expansion of the first and third true-foliage leaves produced was followed through each field season.

Terminal bud scars were used to determine the years of *Nothofagus* stem growth above the *Sphagnum* mat, retrospective annual stem extension, and branching frequency, in the same manner used with *Empetrum*. The vertical height of each stem above the

Sphagnum mat was measured at the end of each season, and compared to the previous field season to calculate the rate of engulfment by *Sphagnum*.

Community composition

Community composition was assessed by placing a quadrat over a 120 × 60-cm area in the center of the plot. The area was divided into 50 equal squares. All the *Nothofagus* ramets and at least two-fifths of the more abundant *Empterum* ramets in the quadrat were censused. The number of years of growth of each ramet above the *Sphagnum* mat was assessed using annual terminal bud scars. Ramets were recruited into "apparent age" classes dependent on whether they were outpacing or being engulfed by the *Sphagnum* mat. This allowed changes in the "apparent age" structure of the *Nothofagus* and *Empetrum* populations to be assessed. The number of *Tetroncium* individuals and the less abundant *N. muscosa, J. scheuchzerioides,* and *P pumila* were counted at the end of the fifth and sixth field seasons of the project.

Statistical analysis

To allow for hydrological gradients and heterogeneity of vegetation across the site, each pair of plots was considered as a block. However, where between-block variability was low, block was omitted from model.

The effect of UV-B treatment on cumulative stem growth, distance between leaf scars on the *Tetroncium* rhizome, morphological characteristics of *Sphagnum* and *Empetrum*, and *Tetroncium* leaf carbon and nitrogen, was assessed using an ANOVA in a one-way factorial, randomized complete block design. The effect of UV-B treatment on *Tetroncium* leaf expansion was assessed using an ANOVA in a one-way factorial,

completely randomized design. The effects of UV-B treatment and year on annual stem and rhizome growth, *Tetroncium* and *Nothofagus* morphological characteristics, change in height growth, and plant population size were assessed using an ANOVA in a two-way factorial, blocked split-plot-in-time design. Year and UV-B treatment were fixed-effects factors, and blocks (where used) were a random-effects factor. The effects of UV-B treatment and apparent age on annual stem growth of *Empetrum* were likewise assessed using an ANOVA in a two-way factorial, blocked split-plot-in-time design. *Tetroncium* rhizome elongation data were Log_e or square-root transformed as appropriate prior to analysis to better meet assumptions of normality and homogeneity of variance. Back-transformed means and standard errors are presented.

We tested various covariance matrix structures: based on the assumption that growth in the peatland at any sampling time was most strongly correlated with growth at the next sampling time, together with Schwarz Bayesian information statistics, we determined that the first-order autoregressive structure was most appropriate for analysis of growing plants; and that the compound symmetry structure was most appropriate for repeatedly-harvested samples. Growth responses of the *Tetroncium* rhizome, and *Sphagnum* capitulum were regressed against temperature, precipitation, and daily UV-B radiation data.

All computations were performed in SAS version 8.2 (SAS Institute Inc., Cary, North Carolina, USA). *P*-values, where given in the text or with figures in ANOVA tables, are accompanied by numerator and denominator degrees of freedom, and F values.

Results

Sphagnum growth

Sphagnum height growth was consistently slightly less (*c* 9%) under near-ambient than under reduced UV-B throughout the experiment (Fig 1). Measurements throughout the growing season showed that most height growth occurred from October to January when the ground-water level is relatively high (data not shown), though this also coincides with maximum ozone depletion.

Capitulum density was slightly increased (*c* 5%) under near-ambient compared with under reduced UV-B, and together with a tendency ($P = 0.062$) for increased capitulum mass (*c* 8%), contributed to an increase (*c* 32%) in volumetric density under near-ambient UV-B (Table 1). This offset the reduction in *Sphagnum* height growth seen under near-ambient UV-B (Fig 1), and resulted in no change in *Sphagnum* biomass production between UV-B treatments (Table 1).

Tetroncium growth

Annual rhizome elongation was reduced (*c* 13%) under near-ambient UV-B (Fig 1). There was no difference ($F_{1,18} = 0.44$, $P = 0.516$) in the magnitude of UV-B effect over the course of the experiment (Fig 2).

Each ramet measured produced five to six leaves per growing season. By measuring elongation between individual leaf scars, we determined that the treatment effect was highly seasonal, most pronounced during periods of rapid growth and not apparent late in the season (Fig 2). No effect on annual root production or the frequency of clonal division was found from rhizome or ramet analysis (Appendix B). *Tetroncium* growth

response to the near-ambient UV-B treatment was significantly negatively correlated with rainfall ($R^2 = 0.894$), but not with other climatic variables (temperature and net radiation).

All measured leaves expanded more slowly under near-ambient UV-B, and reached a smaller final size (*c* 13%) than under reduced UV-B (only Leaf 3 is shown; Fig 3). The number of leaves produced and rate of leaf senescence were not affected by UV-B treatment (Appendix B). There was no change in leaf carbon content (*c* 43% carbon, both treatments; $F_{1,9} = 0.06$, $P = 0.813$), but there was significantly ($F_{1,9} = 8.51$, $P = 0.017$) less leaf nitrogen under near-ambient (2.6 ± 0.1%, mean ± 1 SE) than under reduced UV-B (3.0 ± 0.1%).

Empetrum growth

Annual stem growth of a repeatedly-measured cohort of ramets was consistently reduced from 1999-2002 under near-ambient UV-B (Fig 1). This trend was more pronounced in harvested ramets, representing a range of sizes, over the same period (*c* 10%; Table 2). There was also a slight tendency for less frequent branching and less branch growth under near-ambient UV-B from 1999-2002 (Table 2). *Empetrum* stem growth outpaced height growth of the *Sphagnum* mat under reduced UV-B (Fig 4). However, the increase in *Empetrum* height above the growing *Sphagnum* mat was *c* 53% less under near-ambient than under reduced UV-B (Fig 4).

The apparent age structure of the ramet population above the *Sphagnum* mat also underwent some change due to the UV-B treatments. Ramets with four or more years of growth above the *Sphagnum* exhibited much slower growth than those with fewer years

of growth above the mat. The net result of slow growth of the "older" ramets, and the consistently depressed growth of "younger" ramets under near-ambient UV-B (Appendix B), resulted in 20% of these "older" ramets being partially engulfed by the *Sphagnum* between the 2001 and 2002 growing seasons (Appendix B).

Nothofagus growth

Nothofagus stem growth was highly variable among shoots, and there was no statistically significant effect of UV-B treatment on stem growth (Fig 1). When measured in the sixth field season, there was a decrease in branching frequency (*c* 35%) under near-ambient compared to reduced UV-B (Table 3).

Annual measurements of vertical height show that *Nothofagus* ramets were outpaced by the *Sphagnum* mat. Under near-ambient UV-B *Nothofagus* ramets were engulfed by the *Sphagnum* mat *c* 57% more rapidly than under reduced UV-B (Fig 4).

The UV-B treatments had no effect on *Nothofagus* leaf size or number in November, but in December when fully expanded, the first leaf produced annually was smaller (*c* 15%) under near-ambient than under reduced UV-B (Table 3). There was also a tendency ($P = 0.057$) for fewer leaves (*c* 10%) under near-ambient UV-B (Table 3).

Like *Empetrum,* the growth of *Nothofagus* ramets declined with years above the *Sphagnum* mat (Fig 1). When broken down into apparent age classes, many *Nothofagus* ramets (*c* 50%) had only one year of growth above the *Sphagnum* mat. No changes in the apparent age structure of *Nothofagus* due to solar UV-B treatment occurred during the last two years of the study (Appendix B).

Community composition

Sphagnum annual height growth was greater than that of *Nothofagus* (Fig 4) and *Tetroncium* (Fig 1), but less than that of *Empetrum* in both treatments (Fig 4). Irrespective of the UV-B treatments, *Empetrum* increased (*c* 8%), whilst *Tetroncium* (*c*23%) and *Nothofagus* (*c* 13%) decreased in ramet density from the fifth to the sixth field season (Table 4). However, there were no overall changes in the species composition of the plant community due to the UV-B treatments at the end of the sixth field season (Table 4).

Discussion

Overall, growth of *Sphagnum* and the vascular plant species was reduced by near-ambient UV-B over the last three years of our study. The effects, though small, were generally consistent over time. Many of the trends in measured parameters were not significant when taken in any one year, but were when repeatedly measured over several years.

A reduction in *Sphagnum* height growth and increase in volumetric density to due solar UV-B occurred during the fourth to sixth field seasons and is comparable to that reported during the first three field seasons (Searles *et al.,* 2002). There was no evidence of an incrementally greater treatment effect accumulating with time. A similar change in the growth and morphology occurred in *Sphagnum fuscum* growing under supplemental UV-B lamp treatments (*c* 30% greater than ambient) in a sub-Arctic (68°N) peatland (Gehrke, 1998). In a peatland microcosm study under similarly enhanced UV-B, there

was no effect of the supplemental UV-B on *Sphagnum angustifolium,* and, if anything, a slight decrease in *Sphagnum balticum,* capitulum mass (Niemi *et al.*, 2002a, b).

The most responsive species to UV-B radiation in our study was *Tetroncium,* which exhibited reduced rhizome growth and leaf expansion during the six years of treatments (also see Searles *et al.,* 2002). In other experiments in Tierra del Fuego, near-ambient UV-B similarly reduced summer root-growth in a *Carex* fen (Zaller *et al.,* 2002), and leaf expansion of perennial herb *Gunnera magellanica*, and fern *Blechnum penna-marina* (Rousseaux *et al.*, 1998, 2001). On the Palmer Peninsula, Antarctica, solar UV-B also reduced leaf expansion of *Deschampsia antarctica* (Day *et al.,* 2001) and *Colobanthus quitensis* (Xiong *et al.,* 2002).

Tetroncium favours the wettest areas of the peatland, and in high rainfall years the reduction in rhizome growth under near-ambient UV-B was less pronounced. The UV-B effect was apparently dampened by the greater annual growth under both treatments during wetter years. *Tetroncium* leaf nitrogen concentration was lower under near-ambient than under reduced UV-B. It is possible that these two effects were symptomatic of reduced nutrient availability in low rainfall years. Nutrient limitation is often considered to be the most important stress restricting growth of vascular plants in peatland competition (Aerts *et al.,* 1999; Bridgham, 2002). Even under long-term nitrogen deposition, *Sphagnum magellanicum* monoliths were able to capture and retain most nitrogen in the capitulum, and exhibited reduced height growth and increased density. This, in turn, limited nitrogen availability for the emergent vascular plants (Heijmans *et al.,* 2002a, b).

Empetrum stem growth was consistently reduced by near-ambient solar UV-B during the fourth to sixth field seasons of the experiment. This treatment effect was not apparent during the first three field seasons of the research (Table 2; also see Searles *et al.,* 2002). Generally, *Empetrum* species have been found to be quite unresponsive to climate change factors (Shevtsova *et al.,* 1995; Press *et al.,* 1998; Tybirk *et al.,* 2000; Weltzin *et al.,* 2000). In contrast to our study, there were no long-term effects of supplemental UV-B treatments (*c* 30% greater than ambient) on growth or morphology of *Empetrum hermaphroditum* in a sub-Arctic heath (Gehrke *et al.*, 1996; Phoenix *et al.,* 2001).

In our study, both *Empetrum* and *Nothofagus* were less competitive against the *Sphagnum* mat under near-ambient UV-B. *Empetrum* was less successful at escaping from the *Sphagnum* mat, and *Nothofagus* was engulfed by *Sphagnum* to a greater extent under near-ambient than under reduced UV-B. These trends can only partially be explained by reduced stem growth due to solar UV-B, and it is likely that the concurrent reduction in branching frequency and growth were also contributing factors. Indeed, changes in the production and orientation of branches are known to affect competition between *Sphagnum* and emergent peatland vascular plants (Svensson, 1995). In a comparable study of the effects of solar UV-B on a sub-Arctic heath community, a reduction in branching frequency was the only significant treatment effect on *Empetrum hermaphroditum*, perhaps due to high within-treatment growth variation (Phoenix *et al.,* 2003).

After six field seasons of treatments, changes in growth and competition between *Sphagnum* and vascular plant species were still not reflected at the community level. This

is similar to the results of other solar UV-B manipulation experiments of shorter duration (Day *et al.,* 2001; Phoenix *et al.,* 2003). The only population-level change was the partial engulfment by *Sphagnum* of "older" *Empetrum* ramets subject to near-ambient UV-B for five and six field seasons of treatments. This may indicate that six field seasons is insufficient time for growth effects to be expressed at the community level in such a slow growing system, particularly when many other confounding environmental variables affect growth and competition (Shevtsova *et al.,* 1995; Press *et al.,* 1998).

Our reduced-UV-B treatment is lower than solar UV-B levels in this region before ozone depletion occurred (Searles *et al.,* 2002); therefore, our differences in UV-B treatments were substantially larger than the difference between normal solar UV-B before and with ozone depletion. Yet growth responses of *Sphagnum* and vascular plants to the solar UV-B manipulations were still rather subtle. If ozone depletion in this region substantially ameliorates within the next few decades, it is unlikely that significant changes in the structure of the Tierra del Fuego peatland plant community will occur. In our experiment, *Sphagnum* gained a competitive advantage over emergent vascular plants under near-ambient UV-B, but this was not substantial enough to alter the community composition between the fourth and sixth field seasons of this study. Biomass production of *Sphagnum* was unaffected by UV-B treatments, but hypothetically the change in *Sphagnum* morphology could alter carbon storage by affecting peatland hydrology (van Breemen, 1995), since the denser capitulum layer could retain more water, reducing decomposition in the acrotelm (Malmer *et al.*, 1994). To become meaningful in a broader context, the long-term effects of UV-B radiation should be studied together with

other climatic changes and this has received little attention (Björn *et al.*, 1999; Phoenix *et al.*, 2001; Sonesson *et al.*, 2002).

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Table 1 *Sphagnum magellanicum* morphological parameters.

Parameter UV-B treatment	Capitulum mass (mg mm^{-1} stem length)	Density (stems m^{-2})	Volumetric density (g dm^{-3})	Biomass production (g m^{-2})
Near-ambient	1.38 (± 0.06)	13169 (± 396)	8.06 (± 0.75)	199.2 (± 10.9)
Reduced	1.27 (± 0.05)	12588 (± 380)	6.10 (± 0.69)	191.7 (± 14.5)
P-value	0.062	0.006	0.056	0.625

Samples taken during field season 2001-2002. Mean of ten plots per UV-B treatment (± 1 SE).

Table 2 Retrospective analysis of annual stem and leaf growth and morphology of *Empetrum* ramets.

UV-B treatment	Retrospective analysis of harvested plants (1999-2002)			
	New growth of main stem (mm)	New growth of stem and branches (mm)	Branching frequency (Branches yr^{-1} growth)	Number of leaves (yr^{-1} growth)
Near-ambient	12.4 (± 0.4)	29.0 (± 1.8)	1.2 (± 0.2)	25.8 (± 0.7)
Reduced	13.7 (± 0.5)	34.5 (± 2.2)	1.5 (± 0.1)	28.3 (± 1.3)
P-value	0.044	0.062	0.062	0.114
UV-B treatment	Retrospective analysis of harvested plants (1999-2002)			
	New growth of main stem (mm)	New growth of stem and branches (mm)	Branching frequency (Branches yr^{-1} growth)	Number of leaves (yr^{-1} growth)
Near-ambient	19.0 (± 1.0)	26.1 (± 1.4)	0.7 (± 0.1)	31.1 (± 1.4)
Reduced	19.4 (± 0.9)	27.9 (± 1.9)	0.8 (± 0.1)	34.9 (± 1.9)
P-value	0.664	0.214	0.634	0.124

1999-2002 ramets harvested in February of 2002. 1996-1999 ramets harvested in February of 2000. Data for three field seasons are pooled. Mean of 10 plots per UV-B (± 1 SE).

Table 3 Leaf production and branching frequency of *Nothofagus* ramets.

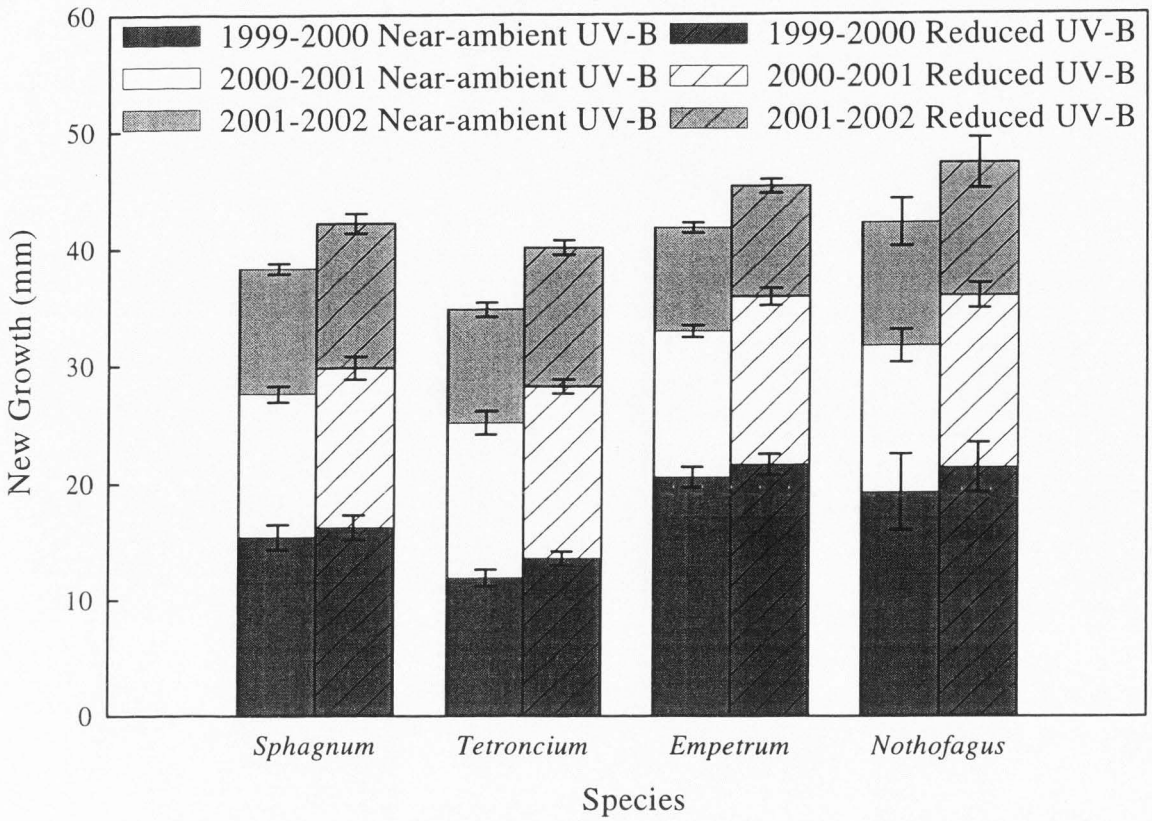
UV-B treatment	Number of leaves on new stem growth (Nov)	Number of leaves on new stem growth (Jan)	Leaf Area – Nov (mm^2)	Leaf Area – Dec (mm^2)	Branching frequency (Branches yr^{-1} growth)
Near-ambient UV-B	3.3 (± 0.2)	4.2 (± 0.2)	1913 (± 123)	3135 (± 123)	1.3 (± 1.1)
Reduced UV-B	3.5 (± 0.2)	4.7 (± 0.3)	2313 (± 236)	3543 (± 186)	1.6 (± 1.1)
P-value					
UV-B	0.355	0.057	0.203	0.044	0.007
Year	0.0001	0.0001	0.0001	0.0001	
UV-B × Year	0.488	0.384	0.271	0.014	

Split-plot ANOVA on data for three field seasons, except branching frequency (2001-2002 only; one-way ANOVA). Mean of 10 plots per UV-B treatment (±1 SE).

Table 4 Annual population of peatland plant species, as total number of ramets above the *Sphagnum* mat per plot over the final two field seasons.

Field season	Species UV-B treatment	*Nothofagus*	*Empetrum*	*Tetroncium*	*Pernettya*	*Nanodea*	*Juncus*
2000-2001	Near-ambient	124 (± 20)	925 (± 175)	434 (± 87)	15 (± 5)	12 (± 4)	29 (± 14)
	Reduced	106 (± 26)	936 (± 142)	443 (± 120)	14 (± 7)	16 (± 3)	17 (± 5)
2001-2002	Near-ambient	108 (± 20)	972 (± 179)	350 (± 85)	7 (± 2)	17 (± 6)	19 (± 8)
	Reduced	93 (± 14)	1059 (± 154)	327 (± 97)	10 (± 3)	16 (± 3)	9 (± 3)
P-value	UV-B	0.360	0.591	0.761	0.766	0.531	0.334
	Year	0.048	0.010	<0.001	0.056	0.347	0.019
	UV-B × Year	0.555	0.269	0.863	0.759	0.055	0.722

Mean of 10 plots per UV-B treatment (± 1 SE).



	Source of Variation	Split-Plot ANOVA *Num df*	*Den df*	*F*	*P*	One-way ANOVA *Num df*	*Den df*	*F*	*P*
Sphagnum growth	UV-B	1	9	4.97	0.027	1	9	5.95	0.037
	Year	2	36	8.95	<0.001				
	UV-B × Year	2	36	0.05	0.951				
Tetroncium growth	UV-B	1	9	6.98	0.022	1	9	6.54	0.031
	Year	2	36	8.15	0.001				
	UV-B × Year	2	36	1.68	0.201				
Empetrum growth	UV-B	1	9	3.66	0.072	1	9	6.28	0.028
	Year	2	36	118	<0.001				
	UV-B × Year	2	36	1.10	0.319				
Nothofagus growth	UV-B	1	9	0.63	0.449	1	9	1.74	0.203
	Year	2	36	16.1	<0.001				
	UV-B × Year	2	36	0.12	0.900				

Fig. 1 Cumulative annual growth increments over three field seasons for the *Sphagnum*, *Empetrum* and *Nothofagus* stems, and the *Tetroncium* rhizome. Each field season mean is for 10 plots per UV-B treatment (± 1 SE). Back-transformed data are shown for *Tetroncium*.

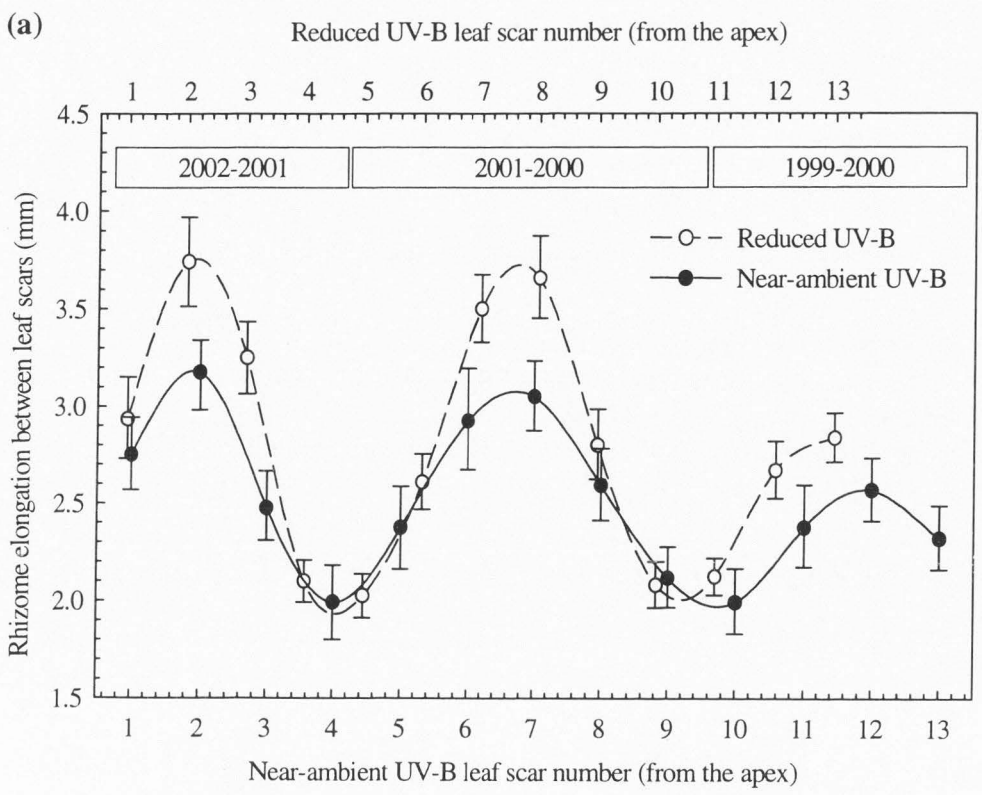


Fig. 2 *Tetroncium* rhizome growth.

(**a**) Rhizome elongation between the most recent 13 leaf scars produced before harvest in March, 2002. Back-transformed means of ten plots per UV-B treatment (± 1 SE) are plotted on two x-axes to allow for differential leaf production under the two treatments. Elongation was significantly reduced under near-ambient UV-B ($P < 0.05$) during the period of maximum growth in each field season.

(**b**) Back-transformed mean annual growth is depicted. Annual elongation was calculated as the distance between tightly clustered leaf scars produced in the autumn of each year. The grey shaded area before 1996 designates growth prior to the UV-B treatments. Inset shows an impression of each individual leaf scar.

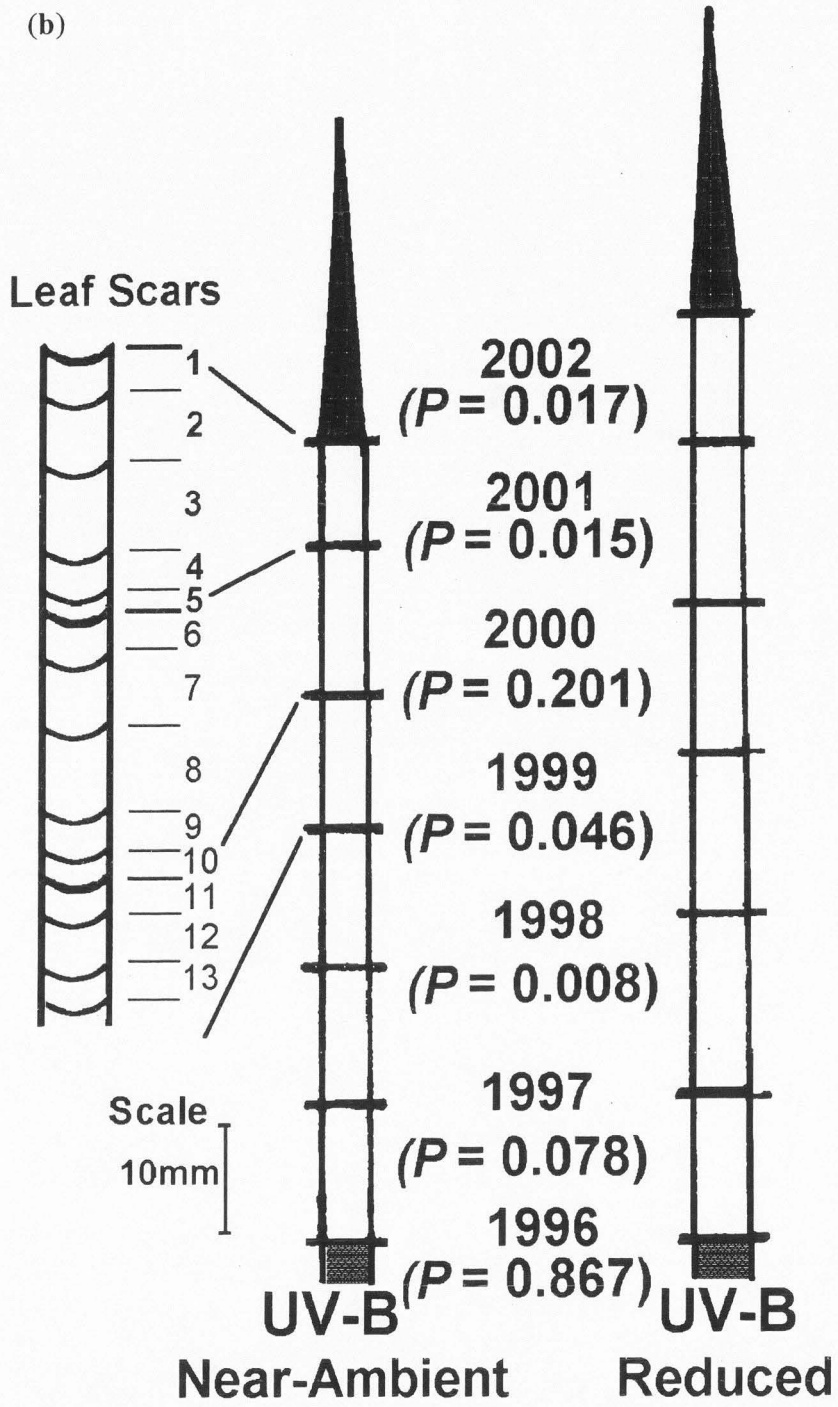
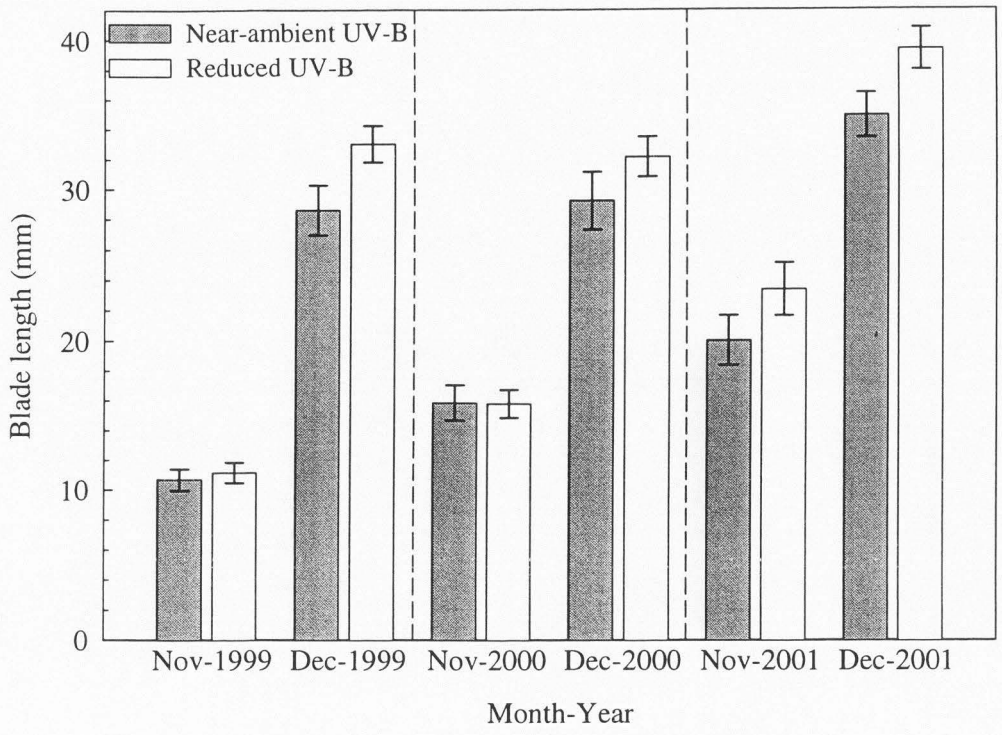
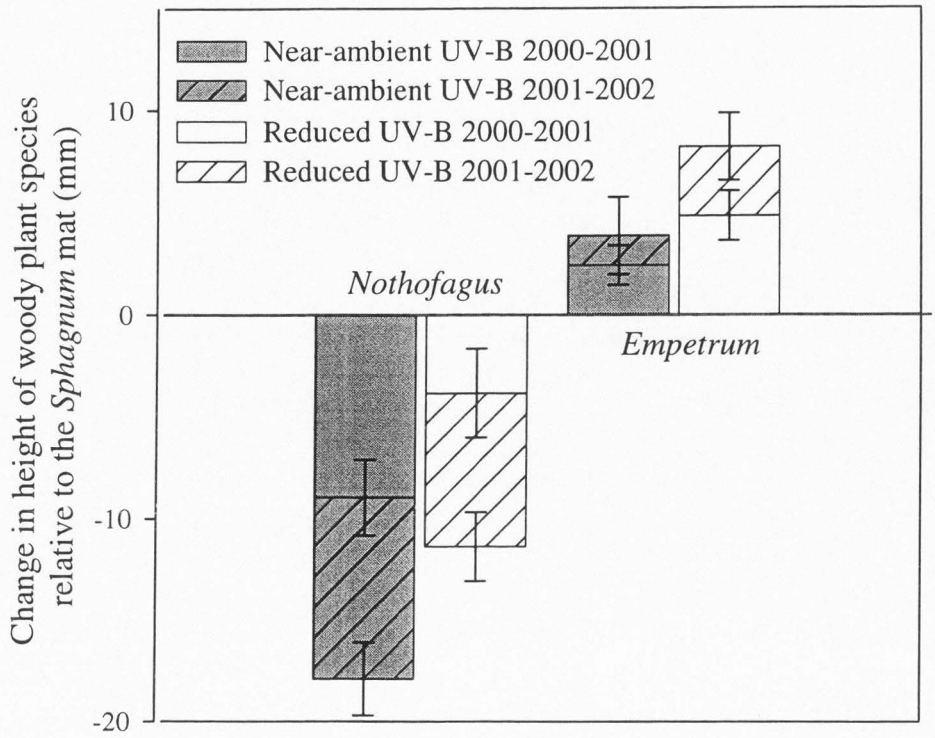


Fig. 2 (continued) *Tetroncium* rhizome growth.



	Source of Variation	*Num df*	*Den df*	*F*	*P*
Tegtroncium leaf 3 (Nov)	UV-B	1	9	1.22	0.298
	Year	2	36	72.1	<0.001
	UV-B × Year	2	36	2.79	0.075
Tetroncium leaf 3 (Dec)	UV-B	1	9	5.76	0.040
	Year	2	36	0.91	0.412
	UV-B × Year	2	36	0.69	0.510

Fig. 3 *Tetroncium* blade length of the third leaf produced. There was a 2-wk interval between the November and December measurement in each year. Mean of 10 plots per UV-B treatment (± 1 SE).



	Source of Variation	*Num df*	*Den df*	*F*	*P*
Nothofagus engulfment	UV-B	1	9	9.63	0.004
	Year	1	18	1.05	0.314
	UV-B × Year	1	18	1.08	0.308
Empetrum escape	UV-B	1	9	8.89	0.006
	Year	1	18	0.65	0.427
	UV-B × Year	1	18	0.03	0.873

Fig. 4 Cumulative annual changes in the height of *Nothofagus* and *Empetrum* ramets relative to the *Sphagnum* mat under near-ambient UV-B and reduced UV-B. Mean of 10 plots per UV-B treatment (± 1 SE).

CHAPTER 3

REDUCTION OF SOLAR UV-B MEDIATES CHANGES IN THE *SPHAGNUM* CAPITULUM MICROENVIRONMENT AND THE PEATLAND MICROFUNGAL COMMUNITY [1]

Abstract

The influence of near-ambient and reduced solar UV-B radiation on a peatland microfungal community was assessed by exposing experimental plots to UV-selective filtration. Replicate plots were covered with special plastic films to effect treatments of near-ambient and attenuated solar UV-B. The microfungal community from the top 1-cm of *Sphagnum* capitulum in a Tierra del Fuego peatland was censused throughout three growing seasons, between 1999 and 2002. *Sphagnum* capitula under near-ambient UV-B were more compressed and held more water than capitula under reduced UV-B. This water had a greater conductivity and was more acidic under near-ambient UV-B, as would be expected with increased leaching from the *Sphagnum* leaves. Nine regularly occurring hyphal fungi from the peatland were identified, at least to genus. Over three field seasons, no treatment effect on total fungal colony abundance was recorded, but individual species abundance was increased (*Mortierella alpina*), decreased (*Penicillium frequentans*), or was unaffected (*P. thomii, Aureobasidium*) by near-ambient UV-B. Species richness was also slightly lower under near-ambient UV-B. These treatment differences were smaller than seasonal or inter-annual fluctuations in abundance and

[1] Co-authored by: T. Matthew Robson, Verónica A. Pancotto, Carlos L. Ballaré, Osvaldo E. Sala, Ana L. Scopel and Martyn M. Caldwell. For publication in *Oecologia.*

species richness. In a growth chamber experiment, lamp UV-B treatments indicated that realistic fluxes of UV-B can inhibit fungal growth in some species. In addition to this direct UV-B effect, we suggest that changes in the peatland fungal community under near-ambient solar UV-B may also result from increased nutrient and moisture availability in the *Sphagnum* capitulum. The subtle nature of the responses of peatland fungi to solar UV-B suggests that most fungal species we encountered are well adapted to current solar UV-B fluxes in Tierra del Fuego.

Introduction

Tierra del Fuego, at the southern tip of South America, has received increased UV-B radiation due to stratospheric ozone depletion for at least the last twenty years (Farman et al. 1985; Frederick et al. 1994). Whilst solar UV-B fluxes often remain low compared to those at low latitudes (about half of mid-summer values at 40° latitude), the relative increase in daily UV-B flux in Tierra del Fuego during the austral spring (October - November) can be up to twice that received prior to the occurrence of ozone depletion (Searles et al. 1999; Rousseaux et al. 1999). This substantial relative UV-B increase may influence community dynamics at different trophic levels in the forests and peatlands that dominate the region, e.g., slower decomposition rate (Pancotto et al. 2003), and changes in the extent of herbivory (Ballaré et al. 2001, Zaller et al. 2003).

Sphagnum mosses in peatlands create the hydrological conditions that allow carbon sequestration to occur through incomplete decomposition (van Breemen 1995; Clymo et al. 1998). Peatlands hold an estimated one-third of global soil organic carbon (Adams and Faure 1998; O'Neill 2000). The importance of peatlands in the global carbon cycle

has spurred considerable research: In particular, the interaction of warming (Gerdol et al. 1998; Weltzin et al. 2001), increased N deposition (Berendse et al. 2001; Tomassen et al. 2003), increased atmospheric CO_2 (Heijmans et al. 2001, 2002), and changing precipitation (Weltzin et al. 2003) on rates of plant growth and decomposition in peatlands (O'Neill 2000) have been investigated. However, few studies have involved the influence of UV-B radiation on processes and organisms associated with decomposition in heaths and peatlands (Searles et al. 2001; Johnson et al. 2002; Johnson 2003).

Water held between leaflets and in hyaline cells of the *Sphagnum* capitulum (dead water-filled cells of the uppermost *Sphagnum* leaflets) provides a niche for the peatland surface microfauna and fungi (Vitt 2000). *Sphagnum*-associated fungi in the acrotelm (Ingram 1978; Belyea 1996), the aerobic layer of the peatland, initiate most of the decomposition of *Sphagnum* (Thormann et al. 2002). Peatland microfungi are also important in the food web of the *Sphagnum* mat (Gilbert et al. 1998, 1999), and serve as a food source for some species of testate amoebae (Coûteaux and Devaux, 1983a, 1983b).

Although the hydrology of the upper few cm's of a peatland is largely dependent on environmental conditions (Bragazza et al. 2003), the volume of water held near the surface is influenced by *Sphagnum* capitulum size and density (Hayward and Clymo 1982). It is not known whether changes in *Sphagnum* capitulum growth and morphology under near-ambient UV-B (Robson et al. 2003) are expressed in the peatland microfungal community.

Microfungal communities are sensitive to changes in acidity and nutrient concentrations in *Sphagnum* capitulum water (Zabawski 1967; Thormann et al. 2003).

Higher concentrations of solutes in the capitulum water, indicated by increased conductivity, under supplemental UV-B, were reported by Niemi et al. (2002a, 2002b). As moss leaves are only one cell thick, they are thought to be particularly susceptible to membrane damage, which leads to cytosolic leakage (Gerdol 1991). Nutrient-binding organochemicals, phenolics, and uronic acid are excreted and leached by *Sphagnum* into the surrounding water (Rasmussen et al. 1995). These lower the pH of the peatland and are inhibitory to some microfungi (Heil et al. 2002), but are utilized by others (Flanagan and Scarborough 1974; Thormann et al. 2002).

From a preliminary microfungal sample in January of 1999, *Mortierella*, *Penicillium,* and *Mucor* were identified as the most abundant genera in the top 1 cm of the *Sphagnum* capitulum (Searles et al. 2001). Species of all three genera are known to respond to UV-B radiation. Supplemental UV-B treatments decreased the abundance of *Mucor* in decomposing leaf litter (Gehrke et al. 1995). Supplemental UV-B inhibited growth of *Mortierella parvispora*, compared to dark controls (Hughes et al. 2003). *Penicillium frequentans* was less abundant on senescent *Gunnera magellanica* leaves (Pancotto et al. 2003) under near-ambient compared to reduced UV-B.

We sampled the peatland microfungi during three field seasons of exposure to near-ambient and reduced UV-B (1999-2002), and concurrently measured plant growth and sampled water from the *Sphagnum* capitulum. We identified the different fungal species in the community where possible, and tracked changes in their abundance to assess the species specificity of response to UV-B. We examined the effect of solar UV-B on fungal diversity, as ubiquitous species were expected to have greater tolerance of UV-B than species native to Tierra del Fuego. We postulated that the combined

effects of UV-B on fungal growth and the altered *Sphagnum* capitulum morphology with associated changes in capitulum water chemistry, could act to alter the microfungal community. To test this hypothesis, we compared responses of cultured fungi in petri dishes with those of the peatland microfungal community under different UV-B treatments. We sampled *Sphagnum* capitula at depths of 0-5 mm and 5-10 mm from the peatland surface. Since solar radiation only penetrates a few millimeters into the *Sphagnum* mat, our goal was to contrast the microfungal community at the peatland surface where it is subject to direct solar radiation, with the community just below the surface where no solar radiation penetrates. We also observed whether the magnitude of response of the microfungal community to near-ambient UV-B followed a similar pattern during three field seasons.

Methods

The study site is a *Sphagnum magellanicum* (Brid) dominated peatland in the Tierra del Fuego National Park (54°51'S 68°36'W).

A weather station and CS 21x datalogger at the site (Campbell Scientific, Logan, Utah, USA) were used to record temperature, precipitation, wind speed, and UV-B radiation throughout each field season. Ambient UV-B (Table 5) and UV-B under the two filter types (data not shown) were measured using broadband global radiation sensors (Solar Light Co., Model PMA2102, Philadelphia, Pennsylvania, USA), calibrated to a double-monochromator spectroradiometer SUV-100 at the Ushuaia UV-monitoring station (Biospherical Instruments, San Diego, USA). Mean temperatures for the 5-month period, October – February, were 8.9°C (1999-2000), 7.9°C (2000-2001), and

9.7°C (2001-2002). Total precipitation for same 5-month period was 260 mm (1999-2000), 312 mm (2000-2001), and 269 mm (2001-2002). Ground water was *c.* 40-cm maximum depth below the surface. The *Sphagnum* mat remained frozen at 5-cm depth through the winter until at least the end of September (for more details of the climate and flora of the peatland see Robson et al. 2003).

Ten pairs of 1.4 × 2.0-m plots were established during October of 1996. Plots were located within an area of relatively homogeneous vegetation without pronounced hummocks and hollows in the *Sphagnum* mat, between a small lake (Laguna Negra) and *Nothofagus* wood. These plots were maintained for the following six field seasons (September – March), and have been used in several long-term field experiments (Ballaré et al. 2001; Robson et al. 2003).

Plastic film filters were stretched (*c.* 40-cm height) over the plots to create the near-ambient and reduced UV-B treatments (see photo Ballaré et al. 2001). A matrix of small louvered slits (*c.* 25 × 2 mm) was melted into the filters prior to installation, to enable water from precipitation to penetrate evenly to the *Sphagnum* mat (Searles et al. 2001). Field trials showed that almost all the precipitation passed equally through the two filter types (unpublished data). Polyester filters (100-µm thick, optically equivalent to "Mylar-D", Dupont Co., Wilmington, Delaware, USA), that attenuate *c.* 83% of short wavelength UV-B radiation (300 nm) were perforated (Searles et al. 2002), were used to achieve the Reduced UV-B Treatment. Polyfluorine filters ("Aclar" type 22A, 38-µm thick, Honeywell, Pottsville, Pennsylvania, USA) that block *c.* 10% of the UV-B (Searles et al. 2002), were used to create our Near-Ambient UV-B Treatment. Both films are equally transparent to longer wavelengths (UV-A and visible), each blocking *c.* 10% of visible

radiation. The UV-B Treatments were randomly assigned within each pair of plots ("block") and remained in place from late September to March each year. This period incorporates early spring when the ozone hole opens but the sun is low in the sky, through to the autumn when UV-B again becomes very low (Díaz et al. 2001). During winter the peatland is usually covered by snow and ice.

The microfungal community, *Sphagnum* capitulum mass, and water held by the capitulum were sampled at four evenly spaced time intervals during the fourth (1999-2000) and sixth (2001-2002) field seasons, and three times during the fifth (2000-2001) field season of long-term UV-B treatments. To avoid edge effects, all samples were taken at least 20 cm from the edge of the area covered by the filters. To accommodate *Sphagnum* surface heterogeneity (Mitchell et al. 2000), a random sample of 28 *Sphagnum* capitula was removed from each plot using sterile forceps. *Sphagnum* capitula were maintained in isolated conditions and taken to the laboratory for immediate weighing and processing.

Under a laminar-flow hood, *Sphagnum* capitula from both near-ambient UV-B and reduced UV-B plots were cut into two 5-mm lengths, corresponding to the 0-5-mm and 5-10-mm depths beneath the surface of the *Sphagnum* mat. Previously, it was established that at least 99% of solar radiation is attenuated at 6-mm depth in the *Sphagnum* capitulum (Searles et al. 1999). The 28 capitula taken from each plot were pooled, weighed, and added to two tubes containing 6 ml of autoclaved deionized water. These tubes were agitated for four minutes, then 400-µl and 200-µl volumes were pipetted onto potato dextrose agar (PDA) under sterile conditions (following Dickinson 1982).

Agar plates were incubated in the dark at room temperature. The various fungal species grew at different rates, so it was necessary to monitor growth from three until eight days after inoculation. Colony forming units (CFU) of each species were counted to determine fungal abundance. Fungal species were identified using Domsch et al. (1980), and additional specific keys for *Mortierella* (Cabello 1997), and *Biverticillium* (Quintanilla 1985).

Ionic conductivity (DIST ATC dissolved solid tester, Cole Parmer, Chicago, Il, USA) and pH (Corning pH-40 sensor, New York, USA) of the 6 ml of water containing the *Sphagnum* capitulum were measured within 12 hours after harvest. Samples were stored in the dark at 4° C until a second measurement of ionic conductivity was taken after 60 hours. Ionic conductivity is considered a good relative indicator of ionic leaching from *Sphagnum* cells (Gerdol 1991). Ionic conductivity was adjusted for H^+ ions following Sjörs (1950). Tests using alcohol to sterilize the sample confirmed that microbial activity did not affect ionic conductivity after 60 hours. On termination of the experiment, *Sphagnum* capitula were oven dried at 65° C for 72 hours and dry mass determined. This allowed the initial water content to be calculated gravimetrically by subtracting dry mass from the initial fresh mass measured directly after capitula were removed from the peatland.

In February of 2003, the most prominent fungal species were isolated from *Sphagnum* capitula. Fungi from near-ambient UV-B and reduced UV-B plots exhibited the same inherent growth rates when inoculated onto petri dishes containing PDA. Cultures were left untreated for two days to confirm that inoculation was successful before UV-B treatments were administered in a growth chamber equipped with a 6000-W xenon lamp.

Daily growth, changes in sporulation, sclerotia, hyphal density, and pigmentation were recorded. The different UV-B treatments were created by replacing most of the petri-dish lid with a plastic filter. As with the solar UV-B treatments in the peatland, polyester film was used to block most of the UV-B radiation, and polyfluorine film allowed the lamp UV-B radiation to pass. A cellulose diacetate filter was wrapped around the lamp to remove radiation <290 nm. The fungi were exposed to 3.5 – 4 kJ $m^{-2}day^{-1}$ UV-B weighted with the generalized plant action spectrum normalized at 300 nm (Caldwell, 1971), measured with a modified double-monochromator (Optronic, Orlando, FL, USA). In Ushuaia, Tierra del Fuego, the average November to February UV-B dose from 1996-2002 was *c.* 4 kJ $m^{-2}day^{-1}$ (Table 5; and Searles et al. 2002), rising to in excess of 8 kJ $m^{-2}day^{-1}$ on the four or five occasions each austral spring when the "ozone hole" passed over the site. Fungal cultures also received *c.* 46.8 mol $m^{-2}day^{-1}$ (800 μmol $m^{-2}s^{-1}$ for 16 hours) of photosynthetically active radiation (total photon flux, 400-700 nm). These daily doses were calculated to approximately simulate our peatland radiation treatments in the field (Zaller et al. 2004).

Statistical Analysis

Species occurrence was calculated as mean presence in the ten plots of each treatment type over the duration of the study (1999-2002). Unadjusted species richness was calculated at the 0-5-mm and 5-10-mm depths, and the Shannon-Weiner index was used to assess evenness of fungal distribution throughout the experiment. The effect of UV-B treatment on each fungal species occurrence, and on species richness was tested using a one-way factorial ANOVA.

To control for the influence of gradients in ground-water depth and pH, and floristic composition across the site, each pair of plots was considered as a block in the statistical models. The effect of UV-B treatment, depth, and month on *Sphagnum* dry mass, water, pH, and conductivity, was assessed using an analysis of variance of a three-way factorial, blocked split-split-plot-in-time design. Ionic conductivity was only measured during the final field season of treatments. Hence, to allow for direct comparison between physical parameters, only results from the final field season are presented for *Sphagnum* capitulum mass, water, and pH.

The abundance of some fungi was low, and there were no distinct seasonal trends in abundance, so abundance data for each field season were pooled before analysis. The effect of UV-B treatment, depth and field season on abundance of each fungal species was assessed using an analysis of variance of a three-way factorial, blocked split-split-plot-in-time design. The UV-B, depth and field season ("Year") were the fixed-effects factors and block, block×UV-B, block×UV-B×depth were the random-effects factors in the design (Aldworth and Hoffman 2002). A first order autoregressive variance/covariance structure for repeated-measures-in-time was determined to be most appropriate for the data (Keselman et al. 2002). To assess the relationships amongst species within the microfungal community, and between fungal species, *Sphagnum* capitulum water and climatic variables, correlations across the ten blocks over the two UV-B treatments, at two depths were used.

The growth chamber experiment was performed twice. Each fungal species was inoculated into four pairs of petri dishes, which were rotated daily under the lamp. Daily measurements of the colony diameter of fungi cultured showed fungal growth to be

constant. Growth rate of each colony was calculated by linear regression, and the mean calculated for each species under lamp UV-B and lamp-UV-B controls. The effect of lamp UV-B on the growth of cultured fungi was tested using a one-way factorial ANOVA in a completely randomized design. All computations were performed in SAS, Version 8.2 (SAS Institute Inc., Cary, North Carolina, USA).

Results

Nine species of hyphal fungi were isolated from the *Sphagnum* capitulum (Fig. 5), of which *Mortierella alpina* and *Penicillium thomii* were the most common. Additionally, several forms of *Aureobasidium* (including *A. pullulans*), a filamentous bacteria *Actinomycetes,* and white and colored yeasts, were isolated from the *Sphagnum* (Fig. 5). There were no significant UV-B effects on occurrence of individual fungal species, except *A. pullulans* which was present in fewer plots under near-ambient UV-B than under reduced UV-B at the 0-5 mm depth (Fig. 5).

Species richness of the microfungal community was slightly lower under near-ambient than under reduced UV-B (Fig. 6). When averaged over the entire sampling period, species richness was significantly lower at 0-5-mm depth from the *Sphagnum* surface under near-ambient UV-B (Fig. 6a; $F_{1,9} = 8.53$, $P = 0.017$), but not at the 5-10 mm depth (Fig. 6b; $F_{1,9} = 1.98$, $P = 0.193$). Shannon-Weiner evenness (J') for the entire 0-10-mm depth was slightly less under near-ambient UV-B in mid-summer (January) during each of the three field seasons (Fig. 6c). This difference was statistically significant if the 11 samples over the three-year period are considered ($F_{1,10} = 15.9$, $P = 0.003$).

Effects of UV-B on the *Sphagnum* microenvironment

Solar UV-B affected *Sphagnum* morphology and properties of the capitulum water (Fig. 7). The *Sphagnum* capitula under near-ambient UV-B held more water than did those under reduced UV-B in our January and March samples (Fig. 7d). This effect was significantly more apparent at the 0-5 mm than at the 5-10-mm depth (Fig. 7d). Higher capitulum dry mass at the 0-5-mm depth under near-ambient UV-B was maintained throughout the growing season (Fig. 7a). Water associated with the *Sphagnum* capitulum was more acidic under near-ambient UV-B in the November and December samples (Fig. 7c). The initial ionic conductivity of *Sphagnum*-capitulum water after harvest was greater under near-ambient UV-B (Appendix B). The rate of increase in ionic conductivity between 24 and 74 hours after harvest was also greater under near-ambient UV-B at three of the four sampling times (Fig. 7b).

Effects of UV-B on fungal species within the microfungal community

Despite a suggestion that abundance of hyphal fungi increased under near-ambient UV-B (Fig. 8, UV-B×Year), the abundance of hyphal fungi in the top 10-mm of the peatland was not significantly affected by solar UV-B when considered over the three field seasons (Fig. 8). However, the overall abundance of fungi did decrease over with time under both treatments (Fig. 8).

The unpigmented species *Mortierella alpina* was more abundant under near-ambient than reduced UV-B (Fig. 9a), but only at the depth of 5-10 mm. At the 0-5-mm depth, no effect of near-ambient UV-B on *M. alpina* was apparent (Fig. 9a). There was no overall

treatment effect on a related pigmented species *M. vinacea*, but it was more abundant under near-ambient UV-B in the 2000-2001 field season (Fig. 9b), suggesting a UV-B × field season interaction. However, when pure cultures of *M. alpina* and *M. vinacea* were subjected to lamp UV-B approximating that of solar UV-B at the peatland surface, there was a reduction of more than 20% in colony growth rate of both species (Table 6).

Two other related species, *P. thomii* and *P. frequentans,* were affected in different ways by near-ambient UV-B. Whilst *P. frequentans* growth and abundance were reduced by both near-ambient UV-B in the peatland and by lamp UV-B in pure culture, *P. thomii* was not affected by UV-B in either experiment (Fig. 9c; d; Table 6). However, an increase in pink sclerotia typical of *P. thomii,* and an apparent decrease in conidial frequency were observed under lamp UV-B, whilst no difference in the conidia of *P. frequentans* was evident.

Abundance in the peatland of the unpigmented species *Mucor hiemalis* under near-ambient UV-B was significantly lower in the final field season of treatments, but unaffected by UV-B overall (Fig. 9e). In pure culture under lamp UV-B, *M. hiemalis* growth was reduced (*c.* 40 %; Table 6), and hyphal density was observed to increase. *Cladosporium herbarum* abundance in the peatland was highly variable amongst years and did not differ between near-ambient (mean CFU ± 1 SE; 0-5 mm 1.89 ± 0.72, 5-10 mm 1.89 ± 0.59 mm) and reduced UV-B (0-5 mm 2.58 ± 0.54 mm; 5-10 mm 1.82 ± 0.50 mm; $F_{1,9} = 0.74$, $P = 0.41$). Colony growth of *C. herbarum* under lamp UV-B was less inhibited than most other species (*c.* 18%; Table 6). *Aspergillus* isolated at 0-5 mm depth in the final field season was less abundant in the peatland under near-ambient (mean CFU ± 1 SE; 0.30 ± 0.10) than under reduced UV-B (0.70 ± 0.19, $F_{1,9} = 6.94$, $P = 0.01$), and in

the growth chamber it was strongly inhibited by lamp UV-B (*c.* 50%; Table 6). Overall, there was no consistent UV-B effect on white or colored yeasts in the peatland, but changes in yeast abundance under the UV-B treatments at the two depths lead to a significant interaction between UV-B and depth (Figs. 9g; h). At the 0-5-mm depth there was a tendency for more yeasts under near-ambient UV-B than under reduced UV-B, whilst at the 5-10-mm depth the opposite tendency was apparent (Fig. 9g; h). *Aureobasidium* abundance was unaffected by UV-B treatment in the peatland (Fig. 9f). Lamp UV-B inhibited *Aureobasidium* growth (Table 6), and accelerated sporulation by approximately two days.

Discussion

To the best of our knowledge, ours is the only Southern Hemisphere peatland microfungal community to have been studied (see also Searles et al. 2001). All the species we encountered are widespread and frequently isolated from Northern Hemisphere peatlands; e.g., in Sweden (Nilsson et al. 1992), Canada (Thormann et al. 2003), and Italy (Dal Vesco 1975). *Penicillium thomii* and *Mortierella* species often dominate microfungal communities near the *Sphagnum* surface (Zabawski 1967; Maciejowska-Pokacka 1971; Dickinson and Maggs 1974; Thormann et al. 2003), and this was also the case in our peatland. In line with Searles et al. (2001), *M. alpina* continued to be the most common species, despite favoring the less acidic areas of the peatland (see also Dal Vesco 1975; Fritze and Bååth 1993).

The response of fungi to our UV-B treatments was species specific (Figs. 8 & 9). Overall fungal abundance was largely unaffected (Fig. 8), but diversity was slightly lower

(Fig. 6) under near-ambient UV-B. These results may indicate that whilst some of the less common species declined under near-ambient UV-B, others, whose growth was relatively unaffected by UV-B, were able to compensate and proliferate (Fig. 9). Additionally, those species that were most abundant under near-ambient UV-B, particularly at the 5-10 mm depth, may have been able to exploit the increased ionic concentration and altered *Sphagnum* capitulum morphology.

Sampling of the microfungal community over three field seasons revealed more effects of near-ambient UV-B than did the initial census of Searles et al. (2001). Often long-term experiments show responses to UV-B that are not apparent in studies of shorter duration (Björn et al. 1999; Phoenix et al. 2001; Day et al. 2001; Pancotto et al. 2003). The detection of UV-B effects on microfungal community composition after several years of treatments is not surprising, given that more changes in the plant community were detected after six years of UV-B treatments (Robson et al. 2003) than during the first three (Searles et al. 1999, 2002). This is particularly true for those fungal species that may respond indirectly to changes in the *Sphagnum* microenvironment brought about by UV-B.

Effects of UV-B on the *Sphagnum* microenvironment and potential consequences for peatland fungi

More water was held at the *Sphagnum* surface under near-ambient than reduced UV-B (Fig. 7). We consider that this was due to the more compressed and densely packed *Sphagnum* capitula under near-ambient UV-B (Robson et al. 2003). Moisture is known to be an important influence on microfungal community composition in peatlands

(Nilsson et al. 1992). Thus, the larger wetter capitula are likely to have provided greater opportunity for fungal colonization under near-ambient UV-B.

The capitulum water was more acidic and had greater ionic conductivity under near-ambient UV-B. These effects of UV-B were not detected over the entire field season, and were not correlated with the volume of water held by the capitulum. Increased ionic conductivity is typically correlated with the leaching of sodium, magnesium, and calcium during the *Sphagnum* growing season, and release of nitrogen and phosphorous during *Sphagnum* senescence in the autumn (Gerdol 1991; Bragazza and Gerdol 1999). Niemi et al. (2002b) attributed increased concentration of calcium and magnesium ions to increased *Sphagnum* membrane permeability under supplemental UV-B radiation. The greater abundance of *M. alpina* and other species under near-ambient UV-B at 5-10-mm depth, and an amelioration of direct UV-B effects for *M. alpina* at 0-5-mm depth in our peatland (Fig. 9a), may be due to the nutritional benefit gained through increased *Sphagnum* membrane permeability under near-ambient UV-B. *Mortierella* are known to break down sugars in initial phases of decomposition in peatlands, and have been shown to respond positively to increased leaching from the *Sphagnum* capitula (Deacon 1997; Thormann et al. 2003).

Decreases in pH and increases in nutrient content in the acrotelm, where most decomposition occurs (Williams and Yavitt 2003), may provide a more favourable environment for the majority of peatland microfungi (Zabawski 1967; Szumigalski and Bayley 1996). Leaching from the *Sphagnum* capitulum is the most significant mass loss during the first phase of decomposition (Thormann et al. 2002), so increased leaching

under near-ambient UV-B could have important implications for decomposition processes.

Effects of UV-B on fungal species within the microfungal community

The active decomposer species *P. thomii* (Thormann et al. 2002, 2003) was the second most abundant species in our microfungal community after *M. alpina*. Its abundance remained unchanged by UV-B during our three-field-season sampling period (1999-2002) and in the initial sample from the peatland in January 1999 (Searles unpublished data). Similarly, *P. thomii* on senesced *Gunnera magellanica* leaves prior to decomposition in a nearby heath was equally abundant under near-ambient and reduced UV-B (Pancotto et al. 2003).

Several investigators have reported *Cladosporium herbarum* to be quite tolerant of UV-B. The occurrence of *C. herbarum* was not significantly reduced by supplemental UV-B (30% above ambient) on the lamina of living oak leaves (Newsham et al. 1997a), though it did decrease during their decomposition (Newsham et al. 1997b). In Tierra del Fuego, *C. herbarum* abundance was not affected by near-ambient UV-B on living *Carex* leaves (Searles et al. 2001), and it increased on *G. magellanicum* leaves under near-ambient UV-B prior to decomposition (Pancotto et al. 2003). In line with these results, the abundance of *C. herbarum* in our peatland was unaffected by near-ambient UV-B, and under lamp UV-B in a growth chamber its colony growth was less inhibited than most other species studied.

It has been suggested that dark pigmentation in *C. herbarum* and other fungi confers protection from UV-B (Pancotto et al. 2003). In Antarctica, pigmentation of some fungal

species in isolated cultures increased in response to ambient UV radiation (Hughes et al. 2003). Also in Antarctica, fewer unpigmented mycelia and conidia were present in the open than under "closed plastic cloches" that reduced UV and increased temperature by 6° C, whereas there were no differences between treatments in the abundance of pigmented soil fungi (Onofri et al. 2000). However, increased solar and supplemental UV-B do not always favor pigmented species of fungi. Supplemental UV-B radiation shifted competitive advantage from unpigmented towards pigmented fungi in only two out of six pair-wise tests of soil fungal species (Duguay and Klironomos 2000). It is difficult to make generalizations about fungal species responses to UV-B as, even within genera, fungi are known to behave differently (Moody et al. 1999). This was the case with the two *Mortierella* species that we encountered (Fig. 9a; b). However, most species of *Penicillium* studied (apart from *P. frequentans*) appear to be tolerant of UV-B. This is illustrated by the apparent lack of effect of UV-B radiation on *P. thomii* abundance in our peatland, also of supplemental UV-B radiation from lamps on *Penicillium brecompactum* in a sub-Arctic peatland (Gehrke et al. 1995), and on *Penicillium* species living on oak leaves (Newsham et al. 1997a). *Penicillium* are generally considered to have high tolerance of environmental stress (Zabawski 1967; Domsch et al. 1980). Some decomposer fungi have been shown to initially respond to UV-B, but these responses were transitory (Gehrke et al. 1995; Newsham et al. 1997a). This may indicate that some species are able to acclimate to higher UV-B radiation.

Conclusions

Changes in the peatland microfungal community under long-term near-ambient UV-B were small and species specific. This was surprising given that there were considerable reductions in growth of fungal cultures under our lamp UV-B treatments. Our peatland UV-B treatments did increase the ionic conductivity, acidity and the volume of water held by the *Sphagnum* capitulum. Perhaps, given that solar UV-B is attenuated quickly at the peatland surface, microenvironmental changes brought about by UV-B were an important influence on the peatland microfungal community. However, this remains to be explicitly tested.

Overall fungal diversity near the surface of the *Sphagnum* was low under both treatments making subtle effects on community difficult to detect. The small decrease in richness recorded may be due to direct inhibition by solar UV-B of less common fungal species, or increased dominance of the most common species in the peatland near-surface microfungal community. This decrease in diversity did not influence the overall fungal abundance, and it appears that most of the fungal species at the peatland surface are sufficiently tolerant of, or protected against, current solar UV-B radiation in Tierra del Fuego. All of the fungi encountered are relatively ubiquitous, and known to live in environments where the UV-B flux is significantly higher than it is in Tierra del Fuego. Alternatively, it is possible that these fungi in Tierra del Fuego have already adapted to the increased solar UV-B radiation that they receive after over two decades of ozone depletion in this region.

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Table 5 Monthly averages of daily integrated solar UV-B radiation over three 5-month field seasons recorded at our peatland field site in Tierra del Fuego National Park (1999-2000, 2001-2002). Data from a nearby fen field site are presented from 2000-2001 courtesy of J.G. Zaller, because of instrument failure at the peatland. The daily UV-B values (kJ m^{-2} day^{-1}) are normalized to one at 300 nm and weighted with the generalized plant action spectrum (Caldwell, 1971). Daily means for each month are shown ± 1 standard deviation among days. Data from the NSF UV-monitoring station in Ushuaia (http://www.biospherical.com/nsf/login/update.asp) are given in parentheses for comparison.

Month	1999-2000	2000-2001	2001-2002
October	2.38 ± 0.68 (2.29)	3.36 ± 2.31 (2.97)	3.22 ± 1.37 (2.32)
November	3.99 ± 1.22 (3.34)	2.57 ± 1.41 (2.60)	2.78 ± 0.99 (2.78)
December	4.48 ± 1.21 (4.62)	4.11 ± 1.97 (3.91)	4.41 ± 1.24 (4.59)
January	4.26 ± 1.10 (4.31)	3.68 ± 1.74 (3.61)	5.75 ± 1.80 (-)
February	2.91 ± 1.00 (2.77)	2.17 ± 0.91 (2.64)	4.11 ± 1.12 (-)
March	No data (1.35)	No data (1.40)	2.23 ± 1.19 (-)

Table 6 Growth rates of fungal species in pure culture under lamp UV-B radiation. Colony growth rate per hour was calculated by linear regression of colony diameter over six days (all R^2 >0.90). The UV-B$^+$ treatment received 3.5-4.0 kJ $m^{-2}day^{-1}$. The UV-B$^-$ treatment received minimal UV-B.

Species	Colony growth rate (mm $hour^{-1}$)		*P* value (*N* = 4)
	UV-B$^-$	UV-B$^+$	
Mortierella alpina	0.482	0.385	0.049
Mortierella vinacea	0.375	0.286	0.024
Penicillium thomii	0.395	0.349	0.539
Penicillium frequentans	0.495	0.370	0.032
Mucor hiemalis	1.354	0.815	0.037
Aureobasidium sp	0.432	0.168	0.034
Aspergillus sp	0.292	0.115	0.008
Cladosporium herbarum	0.234	0.193	0.049

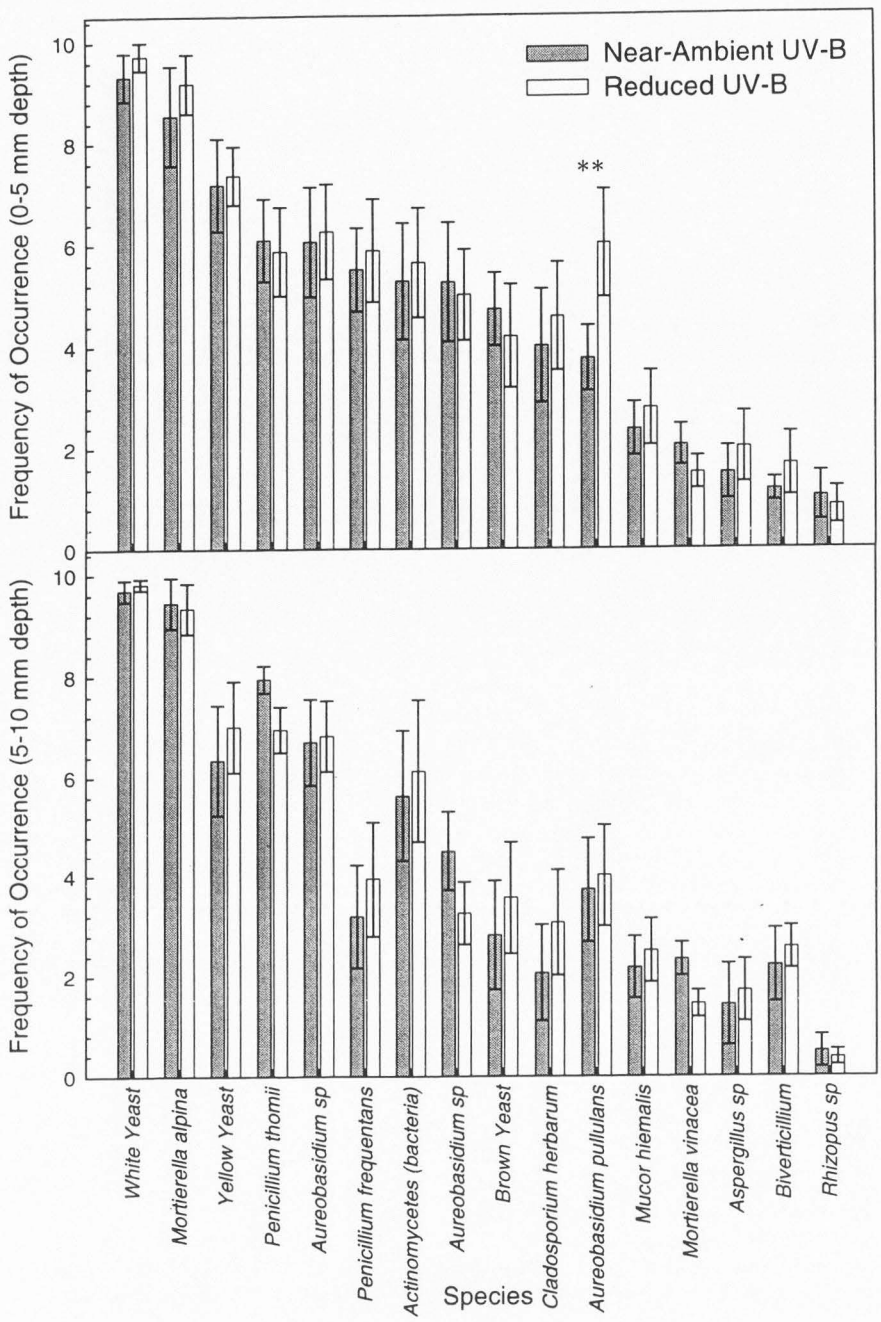


Fig. 5 Frequency of microfungal species occurrence in the *Sphagnum* capitulum, at 0-5-mm and 5-10-mm depth in the peatland. Mean (± 1 SE) number of plots with species present in each UV-B treatment of eleven samples over three field seasons. Species with less than 1-in-10 occurrence, on average, were not assessed. ** signifies $P < 0.01$.

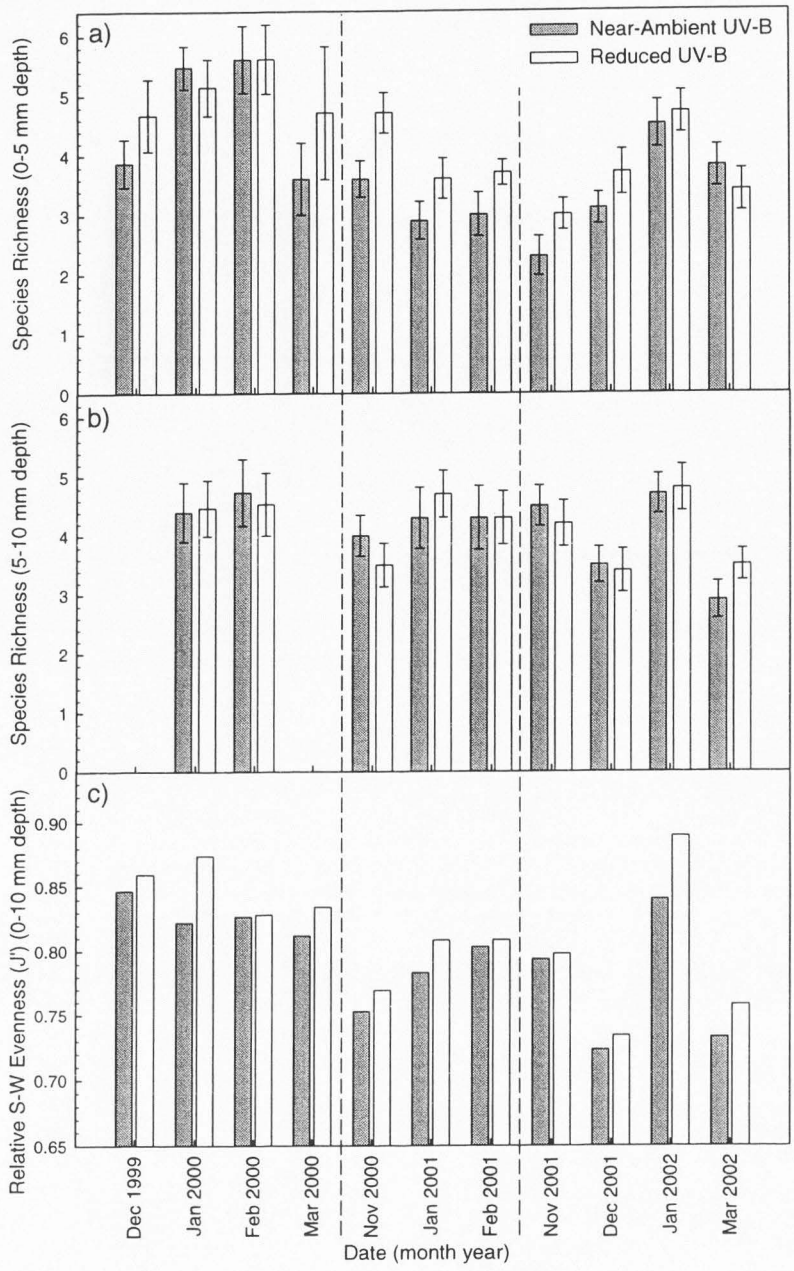
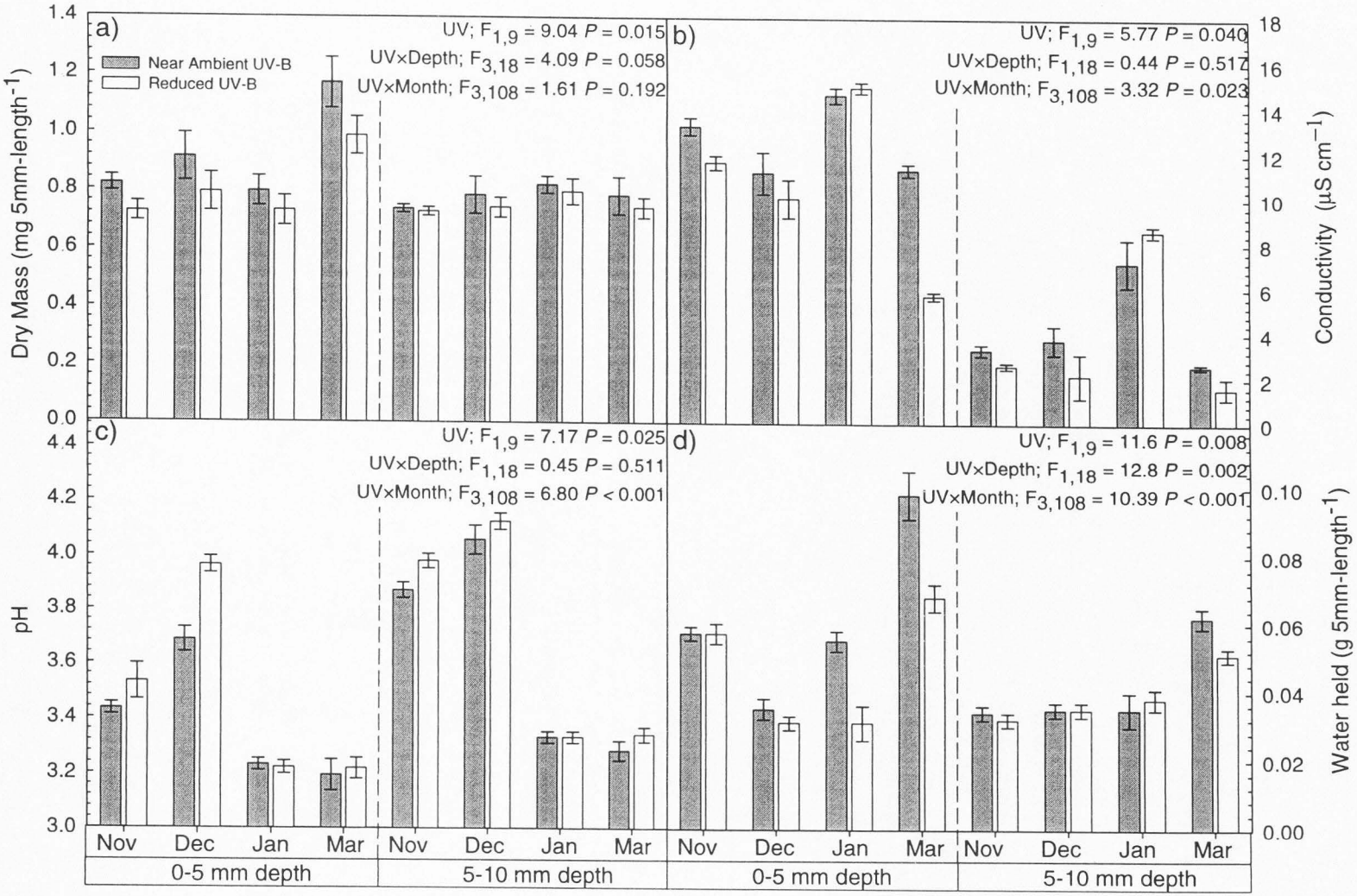


Fig. 6 Fungal Diversity: Mean species richness at; a) 0-5-mm and, b) 5-10-mm depths (± 1 SE) and, c) Shannon-Weiner Evenness (J') at 0-10-mm depth, in the *Sphagnum* capitulum, of ten plots for each UV-B treatment. Diversity was calculated for each of 11 sample dates over three field seasons. In December of 1999, and March of 2000, only the 0-5-mm depth was assessed.

Fig. 7 Physical properties of the *Sphagnum* capitulum. All four of the dependent variables tested demonstrated a significant effect of Month ($P < 0.001$), and Depth ($P < 0.001$). Other sources of variation had insignificant effects. Monthly mean, 2001-2002 field season ± 1 SE: a) *Sphagnum* capitulum dry-mass. b) Change in the ionic concentration of water from the *Sphagnum* capitulum between 24-72 hours after harvest. c) pH of water from the *Sphagnum* capitulum 24 hours after harvest. d) Water held by the *Sphagnum* capitulum.


a)
Near Ambient UV-B
Reduced UV-B
UV; $F_{1,9}$ = 9.04 P = 0.015
UV×Depth; $F_{3,18}$ = 4.09 P = 0.058
UV×Month; $F_{3,108}$ = 1.61 P = 0.192
b)
UV; $F_{1,9}$ = 5.77 P = 0.040
UV×Depth; $F_{1,18}$ = 0.44 P = 0.517
UV×Month; $F_{3,108}$ = 3.32 P = 0.023
c)
UV; $F_{1,9}$ = 7.17 P = 0.025
UV×Depth; $F_{1,18}$ = 0.45 P = 0.511
UV×Month; $F_{3,108}$ = 6.80 P < 0.001
d)
UV; $F_{1,9}$ = 11.6 P = 0.008
UV×Depth; $F_{1,18}$ = 12.8 P = 0.002
UV×Month; $F_{3,108}$ = 10.39 P < 0.001
Dry Mass (mg 5mm-length^{-1})
Conductivity (µS cm^{-1})
pH
Water held (g 5mm-length^{-1})
Nov
Dec
Jan
Mar
0-5 mm depth
5-10 mm depth

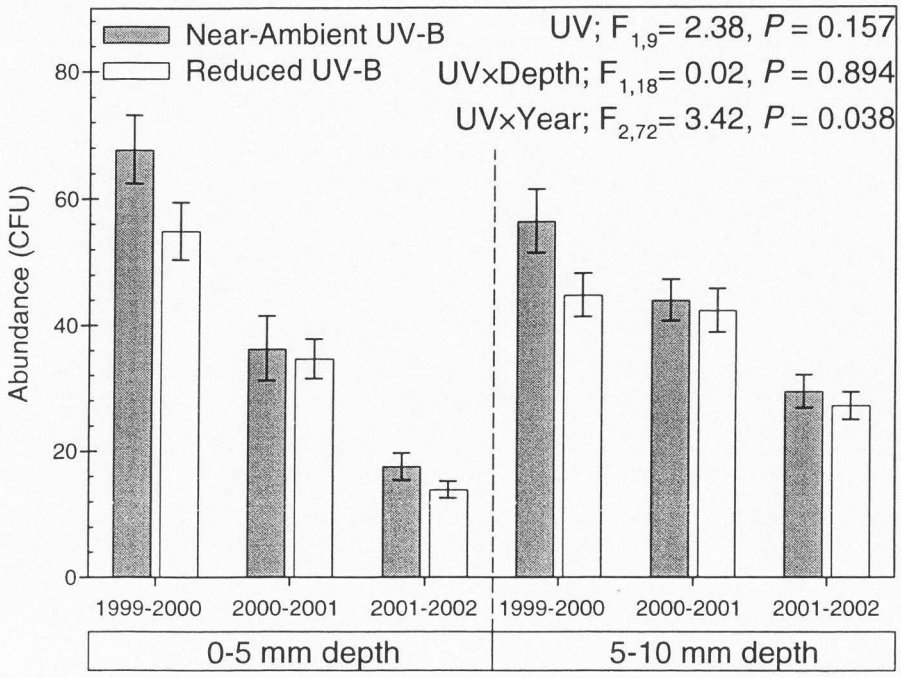
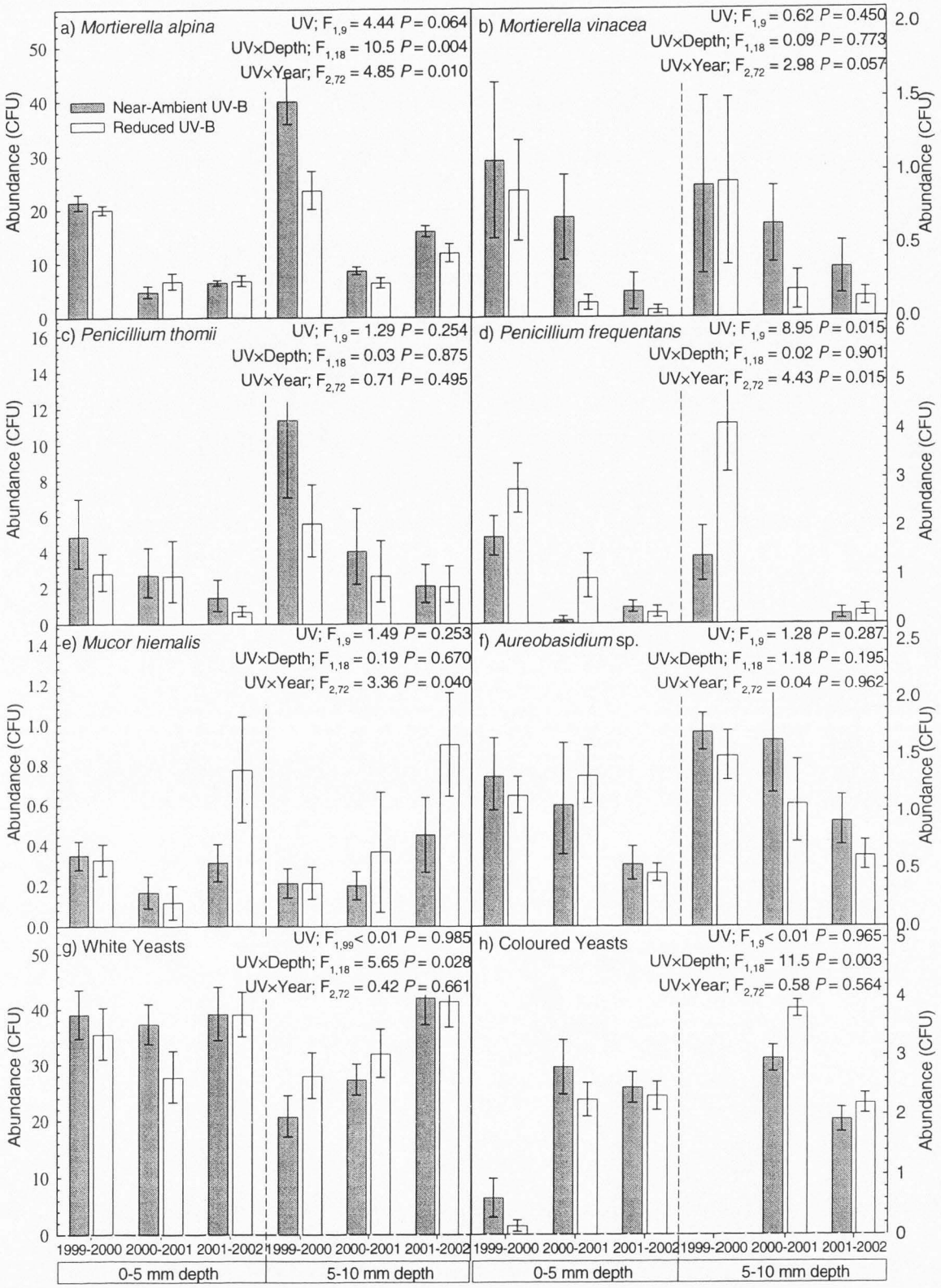


Fig. 8 Abundance of all species of hyphal fungi (colony-forming units). Data represent the back-transformed means (+ 1 SE) of three or four samples pooled over each field season.

Fig. 9 Response of individual fungal species from the peatland microfungal community to near-ambient and reduced UV-B. a) *Mortierella alpina;* b) *Mortierella vinacea;* c)*Penicillium thomii;* d) *Penicillium frequentans;* e) *Mucor hiemalis;* f) *Aureobasidium* sp; g) White yeasts; h) Colored yeasts. The number of CFU per 200 µl from each 6-ml sample containing 14 *Sphagnum* capitula is shown. Back-transformed means (+ 1 SE) of multiple samples (3-4 occasions) for each field season. Three-way interaction terms were all non-significant, except for *P. frequentans*, $F_{2,72} = 3.60$, $P = 0.032$.


a) Mortierella alpina
UV; F1,9 = 4.44 P = 0.064
UV×Depth; F1,18 = 10.5 P = 0.004
UV×Year; F2,72 = 4.85 P = 0.010
Near-Ambient UV-B
Reduced UV-B
b) Mortierella vinacea
UV; F1,9 = 0.62 P = 0.450
UV×Depth; F1,18 = 0.09 P = 0.773
UV×Year; F2,72 = 2.98 P = 0.057
c) Penicillium thomii
UV; F1,9 = 1.29 P = 0.254
UV×Depth; F1,18 = 0.03 P = 0.875
UV×Year; F2,72 = 0.71 P = 0.495
d) Penicillium frequentans
UV; F1,9 = 8.95 P = 0.015
UV×Depth; F1,18 = 0.02 P = 0.901
UV×Year; F2,72 = 4.43 P = 0.015
e) Mucor hiemalis
UV; F1,9 = 1.49 P = 0.253
UV×Depth; F1,18 = 0.19 P = 0.670
UV×Year; F2,72 = 3.36 P = 0.040
f) Aureobasidium sp.
UV; F1,9 = 1.28 P = 0.287
UV×Depth; F1,18 = 1.18 P = 0.195
UV×Year; F2,72 = 0.04 P = 0.962
g) White Yeasts
UV; F1,99 < 0.01 P = 0.985
UV×Depth; F1,18 = 5.65 P = 0.028
UV×Year; F2,72 = 0.42 P = 0.661
h) Coloured Yeasts
UV; F1,9 < 0.01 P = 0.965
UV×Depth; F1,18 = 11.5 P = 0.003
UV×Year; F2,72 = 0.58 P = 0.564
Abundance (CFU)
1999-2000 2000-2001 2001-2002
0-5 mm depth
5-10 mm depth

CHAPTER 4

SOLAR UV-B INFLUENCES MICROFAUNAL COMMUNITY COMPOSITION IN A TIERRA DEL FUEGO PEATLAND[1]

Abstract

The peatlands of Tierra del Fuego are subject to increased solar ultraviolet-B radiation (UV-B) due to the influence of the annual Antarctic "ozone hole" and associated general erosion of the ozone layer. The effect of climate change and ozone depletion on peatlands has predominately focused on the plant community and neglected other organisms. In a six-year experiment, we tested the response of the peatland surface microfaunal community to current and attenuated solar UV-B. This was realized by stretching plastic film filters that differentially attenuate UV-B over peatland sample plots, to create near-ambient and reduced UV-B treatments. We extracted the microfauna of *Sphagnum* capitula removed from the top 1-cm of the peatland. We monitored populations of testate amoebae, rotifers, and nematodes at three time intervals during each field season. We also determined the diversity of testate amoebae under the two UV-B treatments, and sampled water held by *Sphagnum* capitulum for dissolved organic carbon (DOC), nitrate (N), and phosphate (P) content. In line with previous findings in a three-year study in this system, testate amoebae were more abundant under near-ambient than under reduced UV-B. Populations of the most common genus, *Assulina,* and other more variable amoebae species, *Heleopera* and *Euglypha,* were consistently increased by UV-B. Overall diversity and evenness indices of testate amoebae were also higher under

[1] Co-authored by TM Robson, VA Pancotto, AL Scopel, MM Caldwell.

near-ambient than under reduced UV-B. Contrary to the first three-year study, rotifers and nematodes were less abundant under near-ambient UV-B during the current three-year study, as were mites in the final year of the study. Concentrations of DOC and P were generally higher, and there were periodic increases in N, under near-ambient UV-B. These results, and those of the previous study at this site, suggest that changes in the peatland microfaunal community under near-ambient solar UV-B are probably mediated by the plant community, through changes in *Sphagnum*-capitulum morphology and cell leaching, but trophic interactions may also be involved. We suggest that under near-ambient UV-B there is a tendency for metazoa, such as rotifers and nematodes, to decrease, and protozoa and dissolved nutrients to increase. These changes, combined with the changes previously reported in the plant and fungal communities, have the potential to influence peatland carbon storage, and surface nutrient availability.

Introduction

The peatlands of Tierra del Fuego are subject to increased solar ultraviolet-B radiation (UV-B) (Searles *et al.*, 1999), due to the influence of the annual Antarctic ozone depletion that extends over much of southern South America (Orce & Hebling, 1997; Cede *et al.*, 2002). Solar UV-B is known to affect plant growth (Ballaré *et al.*, 2001; Robson *et al.*, 2003), litter decomposition (Pancotto *et al.* 2003), and herbivory (Rousseaux *et al.* 1998, 2004; Zaller *et al.*, 2003) in Tierra del Fuego.

Peatland ecosystems play an important role in global carbon sequestration (Gorham, 1991). They have been studied in the context of general climate change (review: Oechel *et al.*, 2000), and specifically ozone depletion (Gehrke, 1998; Björn *et al.*, 1999; Searles

et al., 1999; 2002; Sonesson *et al.*, 2002), but research has focused largely on the peatland plant community. Like plants, micro-organisms influence the rates of biogeochemical cycling and peatland carbon storage. Testate amoebae, rotifers, and nematodes, are readily observed in water held by the *Sphagnum* capitulum at the peatland surface. The abundance of testate amoebae in peatlands, their short generation time (Schönborn, 1992), and sensitivity to very small-scale environmental changes (Mitchell *et al.*, 2000a) such as conductivity, dissolved nitrogen and carbon, and water table depth (Mitchell *et al.*, 2003), make them good peatland indicator species. Testate amoebae exhibit a more pronounced response than plants to peatland environmental perturbations (Mitchell *et al.*, 2000a), making them useful in the detection of subtle effects before they are expressed by the plant community. Similarly, populations of nematodes (Schröter *et al.*, 2003), rotifers, and peatland metazoa (Hampton, 2004) are known to fluctuate in response to biotic and abiotic environmental changes and trophic interactions.

At the peatland surface, fungi and bacteria initiate the decomposition of *Sphagnum* and vascular plants, and themselves serve as food for testate amoebae and other microfauna (Gilbert *et al.*, 2000; Mitchell *et al.*, 2000a). Complex trophic interactions occur among rotifers, nematodes, and testate amoebae of different sizes, who are themselves food for larger metazoa such as acari mites (Yeates & Foissner, 1995). Dissolved organic carbon (DOC), nitrogen (N), and phosphorus (P) also serve as nutrients at the base of the peatland food web, and their concentrations may be influenced by UV-B indirectly, through leaching from plant tissue and decomposition processes (Moore *et al.*, 1998), and, in the case of DOC, by direct photochemical degradation by UV-B (Tranvik & Bertilsson, 2001).

Previously, we found that *Sphagnum* growth was less affected by solar UV-B than that of vascular plants in a Tierra del Fuego peatland (Robson *et al.*, 2003). Although *Sphagnum* biomass production was unaffected by solar UV-B, carbon storage may still be altered through changes in decomposition. We reported changes in the surface fungal community composition towards species that appear relatively tolerant of solar UV-B. There was also an increase in ionic conductivity and moisture retained by *Sphagnum* capitula under near-ambient compared to reduced UV-B (Robson *et al.*, 2004). Initial studies during the first three years of this long-term experiment (Searles *et al.*, 1999, 2001), revealed that the populations of testate amoebae, rotifers, and nematodes in the top 1-cm of the peatland increased slightly under near-ambient solar UV-B. There were no significant differences in the effects of UV-B treatments between the 0-5-mm depth that receives some solar radiation, and the 5-10-mm depth that does not (Searles *et al.*, 2001). This supports the notion that bottom-up influences, such as increased nutrients and prevalence of certain fungi under near-ambient UV-B, fed through to the microfaunal community.

In this investigation, we continued to monitor the populations of testate amoebae, rotifers, and nematodes under near-ambient and reduced solar UV-B radiation for a further three field-seasons. We investigated seasonal changes through more frequent sampling of the microfaunal community. We identified the species of testate amoebae present in our peatland study site, and assessed their diversity under both UV-B treatments. We monitored nutrients and water held by the *Sphagnum* capitula. We offer a schematic of the changes at different trophic levels that may occur due to UV-B. We

assess the persistence of initial trends in the microfaunal community after six field seasons of UV-B treatments.

Methods

Experimental set-up and treatments

The study site is a *Sphagnum*-dominated peatland in Tierra del Fuego National Park (54°51'S 68°36'W), 20 km to the west of Ushuaia, at the southern tip of South America. Twenty sample plots (2 × 1.40 m) were installed in the peatland during October of 1996, and maintained through each six-month period during the austral spring and summer over the subsequent six years (for more details see Robson *et al.*, 2003). Two UV-B treatments were effected in the plots using special plastic-film filters that differentially attenuate the solar UV spectrum. A reduced-UV-B treatment was achieved using polyester film (optically equivalent to Mylar-D; DuPont Co., Wilmington, Delaware, USA), and a near-ambient-UV-B treatment was achieved using Aclar plastic film (type 22A, Honeywell Co, Pottsville, Pennsylvania, USA). A pattern of small louvered slits (*c* 25 × 2 mm) was melted into every filter before it was stretched horizontally (*c* 40 cm) above each sample plot, allowing precipitation to reach the peatland surface. Field trials showed that almost all the precipitation passed equally through the two filter types (unpublished data). Aclar filters transmit *c* 90%, but polyester filters only *c* 17%, of the short wavelength UV-B spectrum, while both filter types are similarly transparent to longer wavelengths (UV-A and visible) (Searles *et al.*, 2002).

Sampling Sphagnum capitula and extraction of microfauna

Sphagnum magellanicum (Brid.) capitula were sampled from the peatland at three approximately 6-week intervals throughout each field season (1999-2002): at the beginning of November; in mid-December; and late January. Each sample comprised 28 *Sphagnum* capitula removed individually from the entire plot area, excluding a 20-cm strip around the perimeter of the plot to avoid edge effects. This number of capitula was considered sufficient to obtain a representative sample of the microfaunal community in each plot, encompassing microscale heterogeneity, based on the recommendations of Mitchell *et al.* (2000a), and our own field trials.

Sphagnum capitula were maintained in isolated conditions and taken to the laboratory for immediate processing. Previously, Searles *et al.* (1999) established that at least 99% of the solar radiation is attenuated at 6-mm depth in the *Sphagnum* carpet. In an attempt to segregate microfauna exposed to some radiation and to no radiation, *Sphagnum* capitula were cut into two sections corresponding to 0-5-mm and 5-10-mm depths from the upper tips of the *Sphagnum*. The 28 capitula from each depth were added to 12 ml of water, a small sub-sample of which was removed for fungal analysis (see Robson *et al.*, 2004). To standardise our estimate of the microfaunal population among samples, a fixed number of exotic *Lycopodium*-spore markers dissolved in warm water were added to each sample (Stockmarr, 1971, Lund University, Batches #938934, #124961). Individual samples were mechanically vibrated for ten seconds and the solution was strained through a fine mesh. The procedure was repeated with a further 5 ml of water to maximize the extraction of micro-organisms. We consider this procedure adequate to

disassociate the microfauna from the surface of the *Sphagnum* leaves, but probably not sufficient to extract all of those individuals that live within the *Sphagnum* hyaline cells (Mitchell *et al.*, 2003). Thus, our results are likely to be an underestimate of the total microfaunal population.

The strained solution was centrifuged for fifteen minutes (500 *g*) and the supernatant decanted for nutrient analysis. The residue was transferred to 2-ml Eppendorf tubes and re-centrifuged at high speed for 3 minutes to obtain a pellet containing the micro-organisms (adapted from Searles *et al.*, 2001). The supernatant was removed down to 0.25 ml, and three drops of glycerol were added to slow evaporation under the microscope. One drop of the dye Rose Bengal (1% aqueous), which stains cytoplasm red, was added to the samples to aid observation of testate amoebae, rotifers, nematodes, and acari mites.

Microfaunal populations were counted under the microscope relative to the number of exotic *Lycopodium* spores, and adjusted per 10 mg of dry *Sphagnum* (Searles *et al.*, 2001). At least four slides from every plot, each containing one drop of liquid, were counted for each sample.

Testate amoebae were identified to species level where possible. Bdelloïd rotifers (Bdelloidea) were of fairly uniform size and physical characteristics. As with all microfauna, individual nematodes were counted despite their vastly differing sizes. Acari mites and the less frequent of the amoebae species were only counted during the final field season.

Nutrient analysis

Nutrient analysis was performed during the 2001-2002 field season. Following centrifugation of the microfaunal samples, dilutions of the supernatant were prepared for nutrient analysis using deionized distilled water. These dilutions were kept frozen and transported to Utah State University Biogeochemical Laboratory for analysis. In addition to analysis of nutrients from the November, December, and January microfaunal samples, an equivalent sample solely for nutrient analysis was removed late in the field season during March of 2002. Insufficient data were obtained for a comparison of depths in the November N and P samples, so 0-5-mm and 5-10-mm depths were pooled for analysis. Dissolved organic carbon was determined using wet persulphate oxidation (100°C), on an Oceanography International 700 total organic carbon analyzer (Menzel & Vacarro, 1964). Nitrate and phosphate were determined using a DIONEX-500 ion chromatograph with suppressed conductivity detection (Hedin *et al.*, 1998).

Diversity calculations

Two indices of diversity were calculated that incorporated species occurrence and richness of the testate amoebae population under the two treatment types. Simpson's Index (D) measures the probability that two individuals drawn at random from a sample are of the same species, thus gives more weight to the more abundant species in the sampled population. The Reciprocal of Simpson's Index was used to aid interpretation. The Shannon-Weiner Index (H`) measures the uncertainty with which the identity of a species drawn from the population can be predicted; as this value increases, species abundance and richness tend to increase. Both indices also allow the calculation of

heterogeneity / evenness; sampled as a proportion of the (theoretical) maximum species occurrence. In both cases higher values reflect more even distribution of species in the population (Ludwig & Reynolds, 1988; Zar, 1996).

Statistical analysis

Gradients in ground-water depth, pH, and floristic composition across the site led to high spatial variability in microfaunal populations. To control for the influence of these factors, each pair of plots was considered as a block in the statistical models. Microfaunal counts were square-root transformed to better meet the assumptions of normality and homogeneity of variance. The effect of UV-B treatment, depth, and time on the populations of each micro-organism, and on nutrient concentrations, was assessed using an analysis of variance of a three-way factorial, blocked split-split-plot-in-time design (analysis follows Robson *et al.,* 2004). All computations were performed in SAS, Version 8.2 (SAS Institute Inc., Cary, North Carolina, USA). Numerator and denominator degrees of freedom are given in subscript with F and P values for each test.

Results

The population of microfauna, particularly rotifers and nematodes, per dry mass of *Sphagnum* was higher than previously reported under both UV-B treatments (Searles *et al.*, 2001), but we suggest that this was due to improvements in the extraction procedure rather than an actual increase since the first three years. In line with previous findings (Searles *et al.*, 2001), the population of testate amoebae was higher under near-ambient UV-B than under reduced UV-B (Figs. 10 & 11). Diversity of testate amoebae was also higher under near-ambient UV-B (Table 7). This was exhibited both as an increase in

species richness and abundance under near-ambient UV-B at 0-5-mm depth from the *Sphagnum* surface (Table 7). These effects were also reflected in reduced dominance of the most prominent species under near-ambient UV-B, as expressed by the evenness statistics of both Simpson and Shannon Weiner (Table 7).

The microfaunal community composition was similar to that reported for northern peatlands (Tolonen *et al.*, 1992; Mitchell *et al.*, 2000b). Twelve distinct testate amoebae taxa were identified, and the most common were consistent with those previously reported for this site (Searles *et al.*, 2001). In order of abundance these were; *Assulina muscorum* (*c* 25%); *Difflugia oblonga* (*c* 15%); *Assulina semilunulum* (*c* 10%); *Heleopera petroicola* (c 10%); *Euglypha* species (*E. ciliata, E. compressa, E. rotunda*) (*c* 10%); *Nebela* species (*c* 10%); *Corythion dubium* (*c* 5%). *Cyclopyxis arcelloides* (*c* 5%); *Centropyxis aerophila* (*c* 1%); *Hyalosphenia* species (*c* 1%); and *Heleopera syilvatica* (*c* 1%).

Of the testate amoebae, members of the genus *Assulina* increased most in response to near-ambient UV-B (Fig. 10). Though small, the response of *Assulina* to UV-B was consistent throughout the experiment at both depths, particularly in the species *A. muscorum* (Fig. 10), and did not vary seasonally or annually. There was very high spatial variability among pairs of plots, and consequently differences between UV-B treatments at individual sample dates were not significant (Fig. 10). The proportion of empty tests of *Assulina* was very low (consistent with Heal, 1964; Mitchell *et al.*, 2000a), and did not differ between treatments (data not shown).

Two other genera of testate amoebae, *Euglypha* and *Heleopera*, were also more abundant under near-ambient UV-B (Fig 11). Small polyphagous *Euglypha* were

significantly more abundant under both treatments during the fifth field season (2000-2001) than during other field seasons ($F_{2,312} = 215$, $P<0.001$). This may be a result of unusually wet cloudy weather conditions during the fifth field season (Robson *et al.*, 2004). The largely predatory *Heleopera* were more common under both treatments at the lower depth of 5-10 mm ($F_{1,18} = 28$, $P<0.001$), and tended to decrease in abundance over the field season ($F_{2,312} = 15$, $P<0.001$). No effect of UV-B was apparent in the population of *Difflugia oblonga* (Appendix B). Other less common species of amoebae, counted only during the final field season, largely failed to exhibit significant responses to UV-B (Appendix B).

Unlike the first three-year experiment (Searles *et al.*, 1999, 2001), the populations of nematodes and rotifers were significantly reduced under near-ambient UV-B (Fig. 12). The population of nematodes fluctuated significantly with time ($F_{2,312} = 3.3$, $P<0.039$), without exhibiting clear seasonal or annual trends. Rotifers were most common closer to the surface (0-5-mm depth) under both UV-B treatments ($F_{1,18} = 21$, $P<0.001$), and their populations tended to decrease towards the end of each field season ($F_{2,312} = 9.3$, $P<0.001$; Fig. 12). The populations of acari mites were only recorded during the final field season, and as with nematodes and rotifers, were slightly lower under near-ambient UV-B (Fig. 13).

A general increase in the concentrations of DOC and P, but not N, occurred in peatland samples under near-ambient UV-B compared to reduced UV-B during the final field season (Figs. 14 & 15). However, in the November and January samples, N concentration was higher under the near-ambient UV-B treatment (Fig. 15). The increase in DOC under near-ambient UV-B was not apparent in the March sample at the end of

the field season (Fig. 14). The concentration of DOC was higher closer to the peatland surface (0-5 mm) in both treatments ($P>0.001$), and there was no difference in the effect of UV-B at the two depths for any of the nutrients (Figs. 14 & 15).

Discussion

Solar UV-B had a significant effect on the peatland surface microfauna. Abundance and diversity of testate amoebae were consistently promoted under our near-ambient solar UV-B treatment (Figs 10 & 11, Table 7). Populations of rotifers, nematodes, and mites were negatively influenced by near-ambient UV-B (Figs. 12 & 13). The effect on amoebae was consistent over the entire six years of this study, but the change in rotifers and nematodes contrasted with that previously reported (Searles *et al.*, 1999, 2001). The increases in DOC and P support our previous reports of higher ionic conductivity under near-ambient UV-B (Robson *et al.*, 2004).

The composition of the testate amoebae assemblage under both UV-B treatments was similar, but less diverse than commonly reported in *Sphagnum* peatlands (Tolonen *et al.* 1992; Gilbert *et al.*, 1998b; Mitchell *et al.*, 2000a), probably because only the top 1-cm of the peatland was sampled, and diversity is known to increase with depth (Mitchell *et al.*, 2000b). This also supports the view that at higher latitudes richness of testate amoebae declines, as proposed by Ledegenck *et al.* (2003), who linked testate amoebae species richness in grassland ecosystems with plant functional group diversity.

The responses of testate amoebae were species specific, but there was an overall increase in their abundance under near-ambient UV-B. This appears counterintuitive since UV-B is generally considered to be deleterious to organisms. Thus, the increase in

abundance is likely mediated by indirect effects of the UV-B treatments causing the microenvironment in the *Sphagnum* capitulum to be more favorable for testate amoebae under near-ambient UV-B than under reduced UV-B. Growth of the microfaunal community is primarily thought to be limited by the thickness of the water film around *Sphagnum* capitulum leaflets (Mitchell *et al.,* 2003). The small species of testate amoebae that we encountered, *Assulina, Eulgypha,* and *C. dubium,* have flattened tests particularly well adapted to survive in very thin water membranes. *Sphagnum* capitula were wider and more compressed, and consequently held more water under near-ambient UV-B (Robson *et al.*, 2003, 2004), but this is unlikely to have led to a significantly thicker water membrane around each *Sphagnum* leaflet. Un-Spined tests are thought to be adapted for survival in limited water, and *Euglypha* both with and without spines (Bobrov *et al.* 2002) were encountered in both our UV-B treatments.

The *Sphagnum* capitulum ecosystem is complex, and feeding relationships among micro-organisms are not well known (Gilbert *et al.*, 2003). To help interpret the effects of UV-B on the food web, we have formulated a simple schematic outlining expected feeding relationships near the peatland surface (Fig. 16). It is particularly interesting that there was a shift in the microfaunal community towards testate amoebae, but away from the micro-metazoa; rotifers, nematodes, and mites, under near-ambient UV-B. We can suggest several possible forces acting on the microfaunal community under near-ambient UV-B.

It has been suggested that testate amoebae and rotifer populations in the *Sphagnum* capitulum are predominately under top-down control by predation pressure from the peatland metazoa (Mitchell *et al.*, 2003). The reduction we report in the populations of

mites and other predators in the microfaunal community under near-ambient UV-B may lead to a relaxation of top-down control. This release would allow the testate amoebae population to increase. Alternatively, bottom-up food and habitat limitations may also restrict microfaunal population growth (Schröter *et al.*, 2003). Increased nutrient contents in the *Sphagnum* water and large, less elongated, *Sphagnum* capitulum under near-ambient UV-B (Robson *et al.*, 2003), are thought to stimulate bacteria, fungi, and small autotrophs (Gilbert *et al.*, 2000), as reported by Searles *et al.* (1999, 2001). These are the primary food sources for the smaller testate amoebae and rotifers (Pejler & Bērziņš, 1993; Gilbert *et al.*, 2000). However, neither possibility demonstrates why the amoebal population should rise while rotifers and nematodes decrease, when one would expect them to be subject to similar nutritional benefits, under near-ambient UV-B.

Rotifers and nematodes are much more motile than testate amoebae, and actively scavenge for food (Schönborn, 1992). Hence the increased availability of food under near-ambient is likely to benefit testate amoebae more than rotifers or nematodes. Only as more is discovered about the feeding relationships in peatland ecosystems, will it be possible to unravel the reasons for the different responses of specific groups of micro-organisms under near-ambient UV-B.

Solar radiation is attenuated quickly near the surface of the peatland (Searles *et al.*, 2001), and very little solar UV-B is thought to penetrate the *Sphagnum* capitulum. Hence, direct UV-B damage to the peatland microfauna is not likely and most of the influence of UV-B is probably effected by indirect processes. Any direct influence of UV-B over the six years would be likely to affect rotifers more than testate amoebae. This is supported by the more pronounced effect of UV-B on rotifers at 0-5-mm depth.

Amoebae of the genus *Assulina,* exhibit pigmented and non-pigmented test phenotypes. Pigmented tests are physically weaker than unpigmented tests, but their pigmentation may impart some protection from UV-B (Schönborn & Peschke, 1990). Since test morphology varies with the peatland microenvironment (Bobrov *et al.,* 1995), the relative proportion of pigmented and unpigmented tests under near-ambient UV-B and under reduced UV-B might suggest whether direct UV-B effects important for *Assulina* near the peatland surface. Other amoebae species (e.g. *Heleopera* & *Difflugia*) construct their tests from plant material and detritus; these materials may also confer some UV-B protection.

Nematodes and rotifers are transparent to visible radiation and may be transparent to UV (Leech & Williamson, 2000). Studies of the effects of UV-B on lakes and estuarine ecosystems have shown that the motility of ciliates and flagellates, which occupy a similar role in the food web as the peatland micro-metazoa, can be reduced by UV-B (Mostajir *et al.,* 1999). Under supplemental UV-B, this reduction in activity was sufficient to allow increased abundance of their prey and other lower-trophic-level micro-organisms (Mostajir *et al.,* 1999). Ciliate and flagellates were not encountered in our *Sphagnum* capitula, but in rotifer and nematode motility were similarly reduced, this would affect their ability to scavenge and to escape predation. However, so little solar UV penetrates into the peatland that UV-B inhibition of motility may be unlikely in this system.

Effects of UV-B on peatland biogeochemistry

Increased DOC, P, and to some extent N, concentrations under near-ambient UV-B are probably predominantly due to greater ionic leaching from the *Sphagnum* capitulum (Robson *et al.*, 2004). Among the peatland microfauna, testate amoebae make the largest contribution to C and N mineralization (Gilbert *et al.*, 1998a). Thus, an increase in their populations in peatlands under near-ambient UV-B would also be expected to increase decomposition, and release more N to the plant community. But, we were unable to consistently detect an increase in N content of the capitulum water under near-ambient UV-B. Peatland N availability is limited (Malmer *et al.*, 2003), particularly in the Southern Hemisphere where atmospheric deposition is low (Price *et al.*, 2004), so any extra N may have already been utilized.

DOC is important in the peatland carbon cycle and also as a primary food source for the microfauna, fungi, and bacteria. The higher concentration of DOC under near-ambient UV-B than under reduced UV-B may be due to increased leaching from plant material or greater release during decomposition. Direct photochemical cleavage by UV-B may also play a small role in increasing DOC concentration (Tranvik & Bertilsson, 2001). Denser and more compressed *Sphagnum* capitula (Robson *et al.*, 2003) will also increase capitulum DOC under near-ambient UV-B, and if this is sufficient to be transported through the peat to the water table and exported from the peatland, would lead to a reduction in peatland carbon storage.

Conclusions

We conclude that populations of testate amoebae near the peatland surface are slightly, but consistently, increased by UV-B. This effect is probably mediated by the peatland plant community, through changes in the microenvironment and nutrient availability. Given that testate amoebae are considered to be good early indicators of subtle changes in the peatland ecosystem, we would expect them to exhibit a response to UV-B before the plants. Testate amoebae were consistently increased under near-ambient UV-B over the full six-year period, whereas changes in the vascular plants (Robson *et al.,* 2003), rotifers, and nematodes, became apparent only towards the end of the experiment.

The effect of solar UV-B on rotifers and nematodes in the last three years of the experiment differed from that reported by Searles *et al.* (1999, 2001) during the first three years of UV-B treatments. This may be due to an accumulation of subtle effects, such as an increase in competition from testate amoebae; changes in the capitulum microenvironment; or even direct UV-B effects. These reduced populations of rotifers and nemotodes may eventually feed back on their predators, such as acari mites, but given the complexity of the peatland surface food web, it is equally likely that these effects would be negated at higher trophic levels.

The results of this study, combined with the changes previously reported in the plant and fungal communities, show that solar UV-B can alter the peatland ecosystem at many levels. These changes have the potential to influence peatland carbon storage and feed back to increase plant nutrient availability.

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Table 7 Effect of UV-B on testate amoebal diversity.

Species	0-5 mm Depth		5-10 mm Depth		*P*-value		
	Near-Ambient UV-B	Reduced UV-B	Near-Ambient UV-B	Reduced UV-B	$UV\text{-}B_{1,8}$	$Depth_{1,16}$	UV-B × $Depth_{1,16}$
Species Occurrence	72.2 (±3.2)	60.0 (±0.6)	74.1 (±3.8)	69.7 (±2.9)	0.073	0.068	0.195
Species Richness (S)	16.7 (±0.2)	15.3 (±0.3)	14.7 (±0.4)	14.0 (±0.7)	0.021	0.002	0.029
Shannon-Weiner Diversity							
SW Diversity (H')	1.12 (±0.02)	1.08 (±0.02)	1.09 (±0.03)	1.08 (±0.03)	0.018	0.135	0.173
SW Evenness (J')	0.91 (±0.03)	0.86 (±0.03)	0.86 (±0.04)	0.86 (±0.04)	0.024	0.016	0.006
Simpson's Index							
Simpson's Diversity (1/D)	11.5 (±1.2)	10.5 (±1.2)	10.9 (±1.8)	10.9 (±1.1)	0.057	0.706	0.013
Simpson's Equitability (E_D)	0.69 (±0.08)	0.68 (±0.05)	0.74 (±0.07)	0.78 (±0.04)	0.897	0.003	0.381

Mean diversity based on the mean species occurrence on nine sample dates over three field season (± 1 SE).

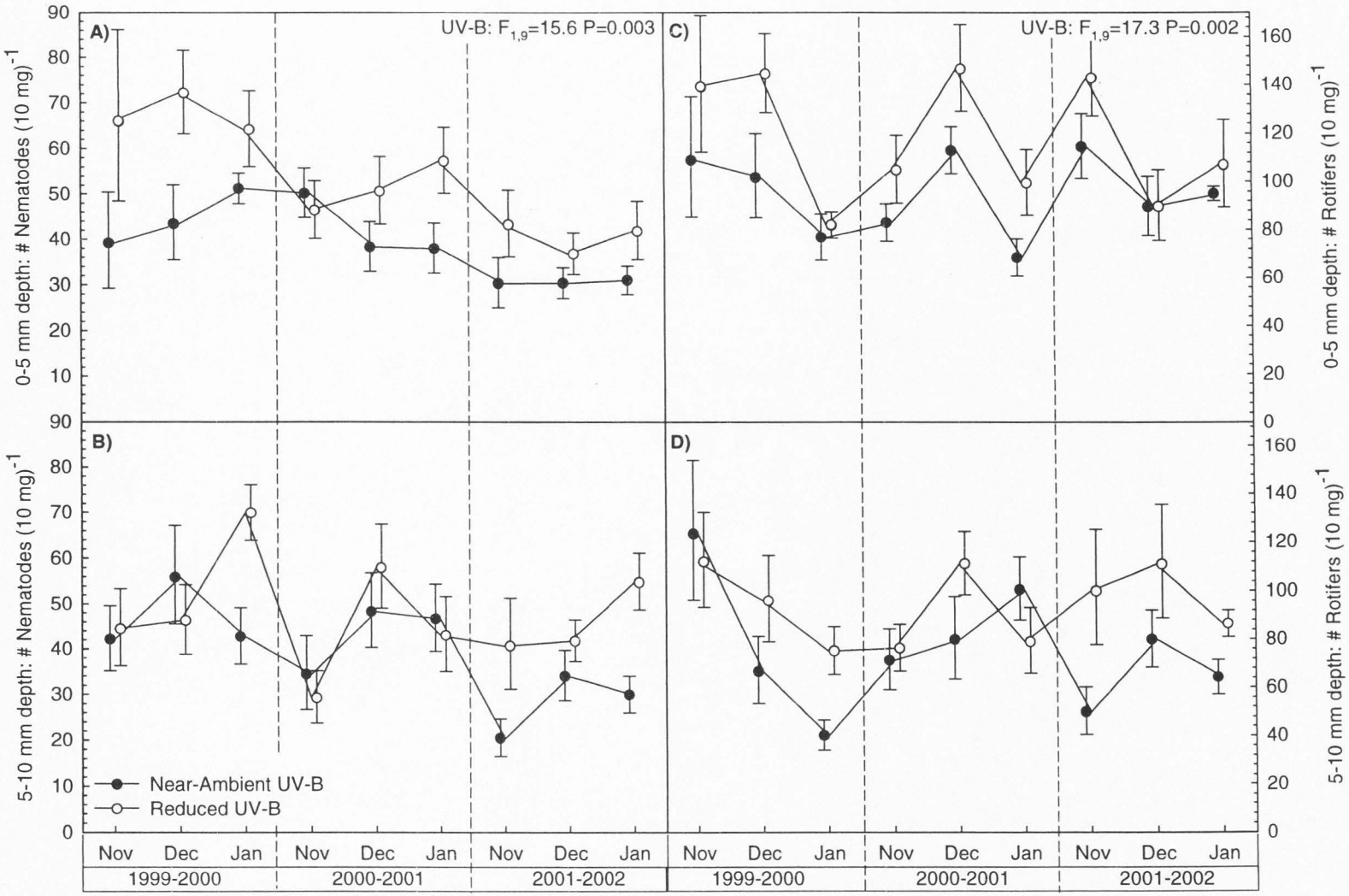
Fig. 10 Trends in the population of testate amoebae under near-ambient and reduced UV-B. *Assulina muscorum* at A) 0-5 mm depth, B) 5-10 mm depth, and all amoebae of the genus *Assulina* including empty tests at C) 0-5 mm depth, & D) 5-10 mm depth. There were no significant interaction effects of UV-B with Depth or Time. The populations of *Assulina* under both treatments decreased with time (Year: $F_{2,213} = 6.5$, $P = 0.002$). Data are back-transformed means ± 1 SE, of the number of amoebae per 10-mg dry mass of *Sphagnum*-capitulum.

A)
UV-B: $F_{1,9}$=4.6 P=0.060
C)
UV-B: $F_{1,9}$=3.7 P=0.084
B)
D)
0-5 mm depth: # *A. muscorum* (10 mg)$^{-1}$
5-10 mm depth: # *A. muscorum* (10 mg)$^{-1}$
0-5 mm depth: # *Assulina* (10 mg)$^{-1}$
5-10 depth: # *Assulina* (10 mg)$^{-1}$
0
10
20
30
40
50
60
70
Near-Ambient UV-B
Reduced UV-B
Nov
Dec
Jan
1999-2000
2000-2001
2001-2002

Fig. 11 Trends in the population of testate amoebae under near-ambient and reduced UV-B. *Euglypha* species, including *E. compressa, E. rotunda* & *E. cilata*, at A) 0-5 mm depth, & B) 5-10 mm depth, and amoebae of Genera *Heleopera* at C) 0-5 mm depth, & D) 5-10 mm depth. There were no significant interaction effects of UV-B with Depth or Time on *Euglypha*. Under both treatments, *Euglypha* populations were higher during the 2000-2001 field season (Year: $F_{2,213} = 215$, $P < 0.001$), and showed significant seasonal variability (Month: $F_{2,213} = 9.4$, $P = 0.001$). The UV-B effect on *Heleopera* was more pronounced at 5-10-mm depth (UV × Depth: $F_{1,18} = 3.4$, $P = 0.082$), where they were more abundant overall (Depth: $F_{1,18} = 28$, $P < 0.001$). The amoebal population under both treatments also varied significantly over time (Month: $F_{2,213} = 26$, $P < 0.001$). Data are back-transformed means ± 1 SE, of the number of amoebae per 10-mg dry mass of *Sphagnum*-capitulum.

A)
Near-Ambient UV-B
Reduced UV-B
UV-B: $F_{1,9}$=4.3 P=0.067
C)
UV-B: $F_{1,9}$=5.0 P=0.052
B)
D)
0-5 mm depth: # *Euglypha* (10 mg)$^{-1}$
5-10 mm depth: # *Euglypha* (10 mg)$^{-1}$
0-5 mm depth: # *Heleopera* (10 mg)$^{-1}$
5-10 mm depth: # *Heleopera*(10 mg)$^{-1}$
0
5
10
15
20
25
30
Nov
Dec
Jan
1999-2000
2000-2001
2001-2002

Fig. 12 Trends in the population of nematodes at A) 0-5-mm, & B) 5-10 mm depth, and rotifers at C) 0-5-mm, & D) 5-10-mm depths under near-ambient and reduced UV-B. There was significant variability in the nematode populations among months under both treatments (Month: $F_{2,213} = 9.4$, $P = 0.001$). The UV-B effect on rotifers was more pronounced at 0-5-mm depth than at 5-10-mm depth (UV × Depth: $F_{1,18} = 21$, $P < 0.001$). The rotifer populations under both treatments also decreased during the field season (Month: $F_{2,213} = 9.3$, $P = 0.001$). There were no other significant effects of UV-B with Depth or Time on either nematodes or rotifers. Data are back-transformed means ± 1 SE, of the number of micro-metazoa per 10-mg dry mass of *Sphagnum*-capitulum.


A)
UV-B: $F_{1,9}$=15.6 P=0.003
C)
UV-B: $F_{1,9}$=17.3 P=0.002
B)
D)
0-5 mm depth: # Nematodes (10 mg)$^{-1}$
5-10 mm depth: # Nematodes (10 mg)$^{-1}$
0-5 mm depth: # Rotifers (10 mg)$^{-1}$
5-10 mm depth: # Rotifers (10 mg)$^{-1}$
Near-Ambient UV-B
Reduced UV-B
Nov Dec Jan Nov Dec Jan Nov Dec Jan
1999-2000 2000-2001 2001-2002

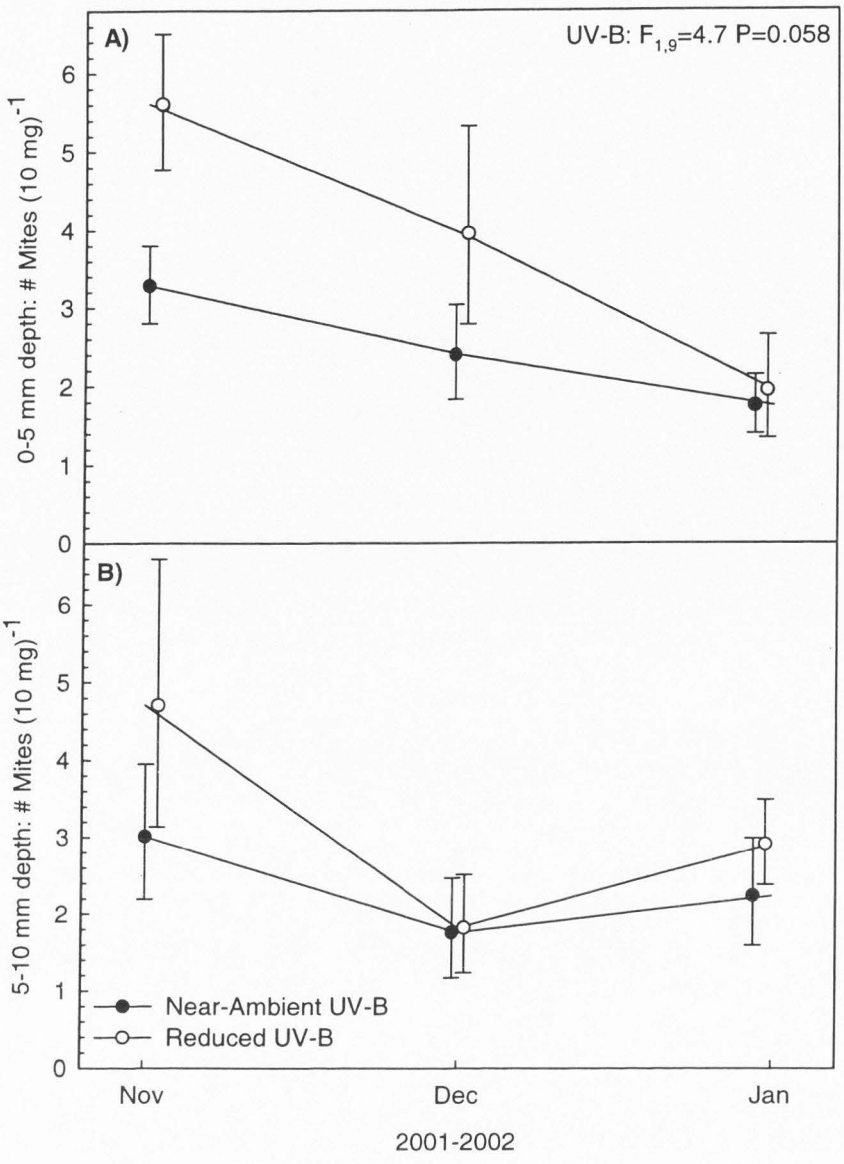


Fig. 13 Trends in the population of acari mites (Acari: Oribatida) under near-ambient and reduced UV-B at A) 0-5-mm depth, and B) 5-10-mm depth. The population under both treatments was significantly higher during November than at other sampling times (Month: $F_{2,72} = 5.9$, $P = 0.004$). There were no significant interaction effects of UV-B with Depth or Time. Data are back-transformed means ± 1 SE, of the number of acari mites per 10-mg dry mass of *Sphagnum*-capitulum.

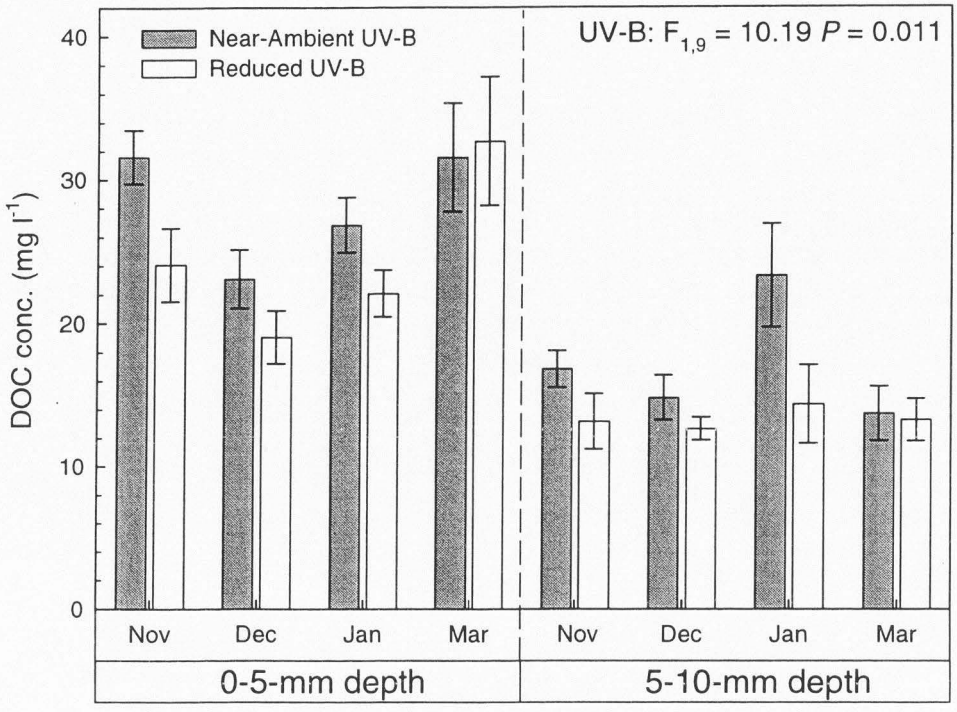


Fig. 14 Concentration of dissolved organic carbon (DOC) in the *Sphagnum* -capitulum water under near-ambient and reduced UV-B, during the sixth field season (2001-2002). The concentration is calculated from standardized 1 ml of water removed from each sample. There were no significant interaction effects of UV-B with Depth or Time on DOC concentration. Under both treatments, DOC was more concentrated closer to the surface ($F_{1,9} = 90$, $P < 0.001$). Data are means ± 1 SE, of the DOC concentration (mg l^{-1}) in each sample of 28 *Sphagnum* capitulum in 1 ml water.

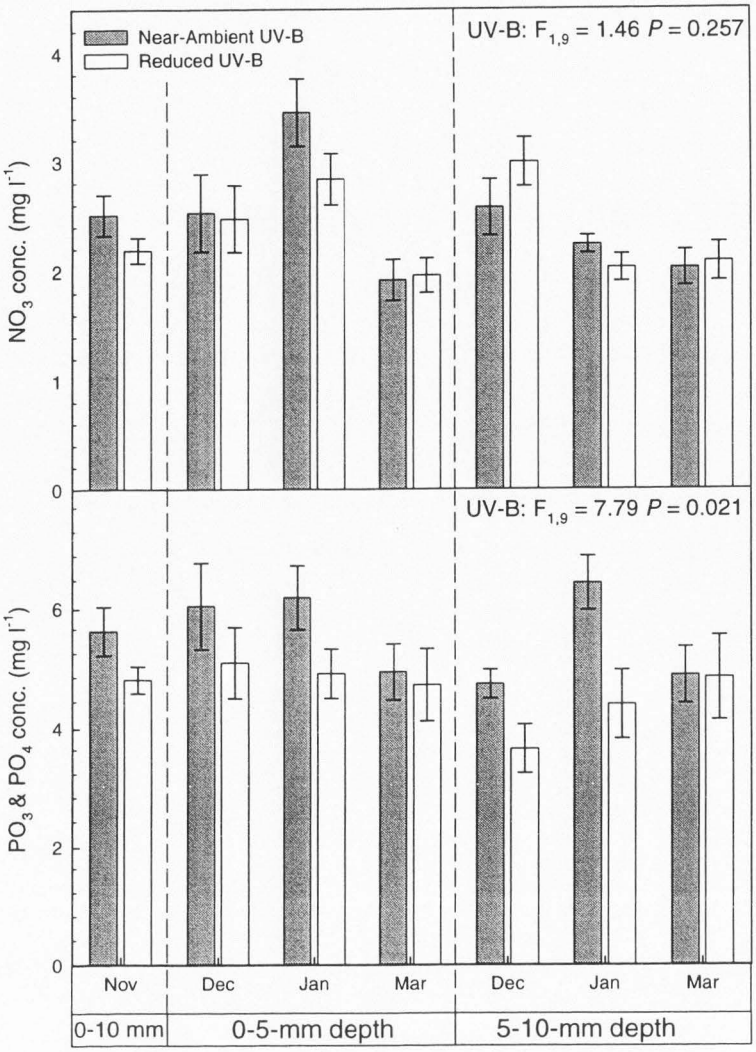
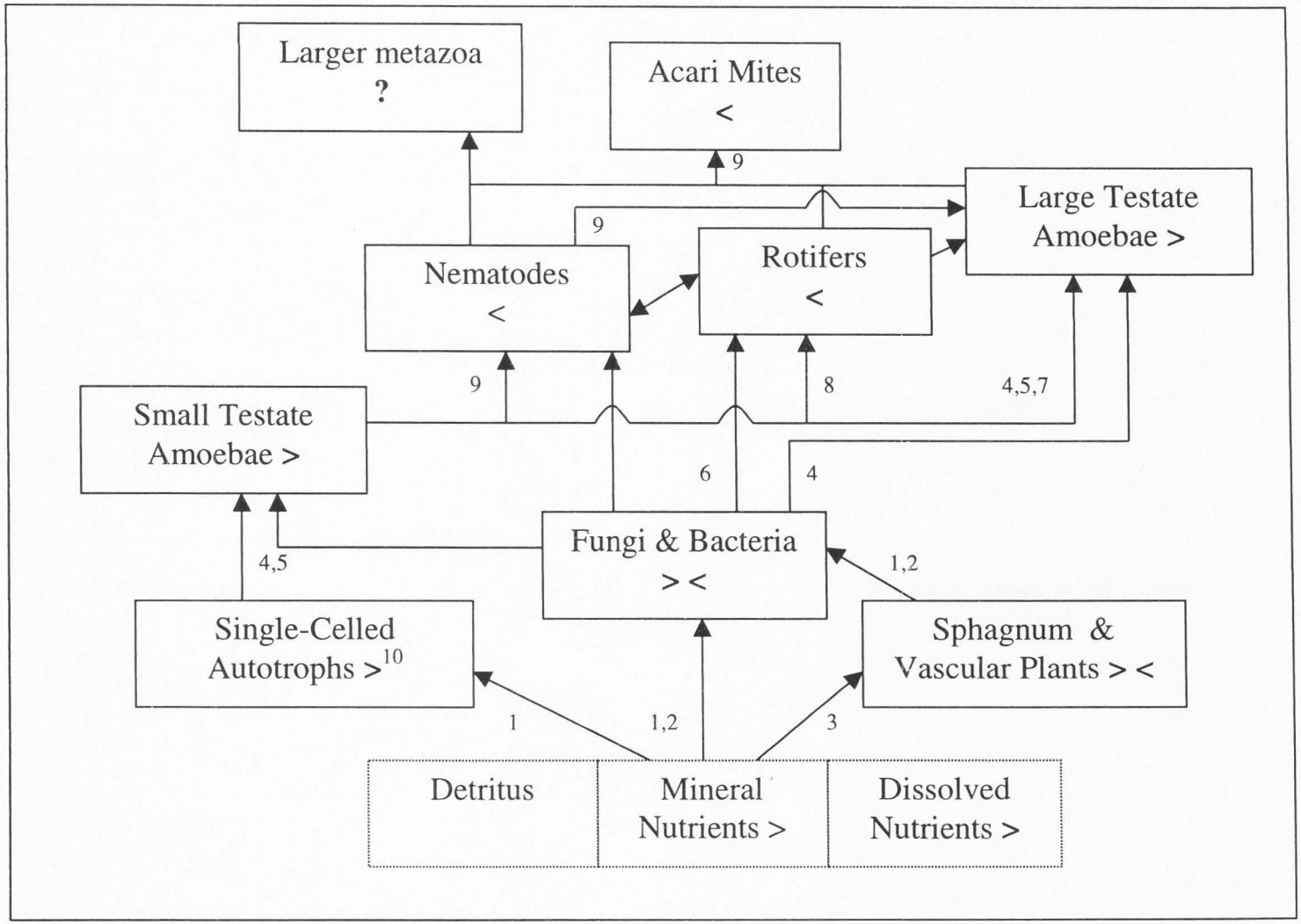


Fig. 15 Concentration of nitrate (NO_3) and phosphate (PO_3 PO_4) in the *Sphagnum* capitulum water under near-ambient and reduced UV-B, during the sixth field season (2001-2002). The concentration is calculated from standardized 1 ml of water removed from each sample. There were no significant interaction effects of UV-B with Depth or Time on nitrate and phosphate concentration. The concentrations of nitrate in November ($F_{1,9}$ = 3.6, P = 0.09) and January ($F_{1,9}$ = 4.9, P = 0.05) alone were higher under near-ambient UV-B. Data are means ± 1 SE, of the N & P concentrations (mg l^{-1}) in each sample of 28 *Sphagnum* capitulum in 1 ml water.

Fig. 16: Simple schematic model of the peatland near-surface ecosystem. Arrows represent the direction of feeding among the major components of the peatland ecosystem; double-headed arrows signify when these interactions can occur in both directions. Decomposition of all organisms returns nutrients and detritus to the system, and is not explicitly illustrated. Information on food web relationships was obtained from: 1. Gilbert *et al.* (2003), 2. Thormann *et al.* (2003), 3. Bragazza *et al.* (2003), 4. Gilbert *et al.* (2000), 5. Coûteaux & Pussard (1983), 6. Pejler & Bērziņš (1993), 7. Schröter *et al.* (2003), 8. Weisse & Frahm, (2001), 9. Yeates & Foissner, (1995). The effects of UV-B from this investigation and the first three years of this experiment (10. Searles *et al.*, 2001) are given in the boxes. Groups that decrease with UV-B are represented by < or <<; those that increase with UV-B; >, groups that show mixed response to UV-B, > <; and those that were not investigated by, ? .


Larger metazoa
?
Acari Mites
<
9
Large Testate
Amoebae >
9
Nematodes
<
Rotifers
<
9
8
4,5,7
Small Testate
Amoebae >
6
4
Fungi & Bacteria
>
<
4,5
1,2
Single-Celled
Autotrophs >10
Sphagnum &
Vascular Plants > <
1
1,2
3
Detritus
Mineral
Nutrients >
Dissolved
Nutrients >

CHAPTER 5

SUMMARY AND CONCLUSIONS

Experiments that manipulate solar UV-B to create near-ambient UV-B and reduced UV-B treatments have been performed at various high latitude sites. The scope of investigations into the effects UV-B in Antarctica has been limited to individual species of vascular plants (Day *et al.*, 2001) and bryophyte (Newsham, 2003). In the Northern Hemisphere, heaths (Phoenix *et al.*, 2002) and peatlands (Niemi *et al.*, 2002a) inside the Arctic Circle (66.5° N) have been investigated. The location of my group's experiments in Tierra del Fuego, though not as close to the poles as others', enabled us to investigate more complex ecosystems than occur in Antarctica. Tierra del Fuego, at 55° South, is amongst the regions most influenced by ozone depletion, which has continued to be more pronounced in the Southern Hemisphere than in the Northern Hemisphere (Solomon, 2004). Although peatland ecosystems are not common in the Southern Hemisphere, their composition is functionally very similar to those in the Northern Hemisphere: This enables valid cross-hemispheric comparisons to be made.

During the three years from 1999 to 2002 ozone depletion continued to occur over Antarctica and Tierra del Fuego (Solomon, 2004). This included several days during the austral spring in 2000 and 2001 when the ozone hole was directly over Tierra del Fuego (Appendix A). Although the weather was quite variable among field seasons (Appendix A), the relative consistency of ozone depletion from 1996 to 2002 allows my three field seasons of data (1999-2002), to be compared with the previous three field seasons (1996-1999) (Searles, 2000).

Since the inception of this experiment there have been subtle changes in the patterns of Southern Hemisphere ozone depletion. Initial predictions were for ozone depletion to reach a maximum close to 1999 (Madronich *et al.,* 1998). However, more recent analyses are increasingly uncertain about the rate of recovery, given possible interactions with stratospheric cooling (Shindell *et al.,* 1998; Roscoe & Lee, 2001; Rex *et al.*, 2004). In the austral springs of 2000 and 2001 the ozone hole appeared earlier than anticipated, and in 2002 the hole unexpectedly divided in two and moved away from Antarctica early in the spring (Solomon, 2004). The recent tendency for increased early spring UV-B has caused large daily fluctuations of up to a 100% increase from a normally very low UV-B. This may be ecologically important as it would result in plants receiving unusually high UV-B coinciding with the initiation of growth in the spring, when temperatures are cool and UV-B doses have been low historically. Such a change may have a greater direct impact than later season UV-B on the native flora of Tierra del Fuego. Cyclobutane pyrimidine dimers (CPD's) in DNA, caused by UV-B radiation, undergo light dependent photorepair (Mazza *et al.*, 1999). This mechanism is somewhat temperature dependent (Takeuchi *et al.*, 1996; Li *et al.* 2002), thus, thought to be less efficient at the start of the growing season when temperatures are low (Giordano *et al.,* 2003). Native herb *Gunnera magellanica* has a low DNA repair capacity: CPD's have been shown accumulate in its leaves during the early spring, coinciding with slower leaf expansion under near-ambient compared to under reduced UV-B radiation (Giordano *et al.,* 2003). Phenolic UV-B screening pigments are also thought to mitigate the harmful effects of UV-B radiation (Ballaré *et al.*, 2001). A seasonal accumulation of phenolic UV-B screening compounds occurs through spring and early summer in the leaves of

native *Nothofagus* species (Robson *et al.*, 2000). The importance of these two responses to UV-B is likely to be increased if ozone depletion continues to occur earlier in the austral spring.

The peatland sample plots received either *c* 90% of solar UV-B (near-ambient UV-B), or *c* 17% of solar UV-B (reduced UV-B). Thus, the reduced UV-B treatment transmitted much less UV-B than was received prior to ozone depletion. The UV-B treatments were selected to incorporate natural variability in solar radiation and be sufficiently large to allow identification of subtle individual responses of UV-B. Ideally the experiment would simulate current and pre-depletion doses of UV-B. However this presents practical problems, because the magnitude of responses to UV-B generally reported indicates that effects of UV-B would be very difficult to detect under a more conservative UV-B treatment; also because it is difficult to create a realistic reduced UV-B treatment that only filters a small portion of the total solar UV-B.

In Chapter 2, I report an increase in *Sphagnum* capitulum width and density and a decrease in height growth, similar to that occurring under near-ambient UV-B during the first three field seasons of treatments (Searles *et al.*, 2002). A slight decrease in the stem and height growth of vascular plants emerging from the *Sphagnum* carpet under near-ambient UV-B also occurred. This differs from the results of the first three field seasons, when no effect was reported (Searles *et al.*, 2002). There are at least three possible explanations for this inconsistency: 1) that denser cover of *Sphagnum* intercepted more nutrients under near-ambient UV-B, thus restricting nutrient availability to vascular plants; 2) that the cumulative effects of (the attenuation of) UV-B under the filters meant that this subtle change, that was too small to be detected after just three field

seasons, became apparent after six; 3) that more exacting analysis and intensive sampling allowed this treatment effect to emerge. The first explanation is the most interesting, and is supported by evidence: There was reduced productivity of *Empetrum* and *Nothofagus* stems with several years of growth above the *Sphagnum* carpet. Despite the changes that occurred in the populations of *Empetrum* and *Nothofagus* there was no difference in plant community structure due to UV-B treatment. Perhaps with further years under the UV-B treatments, community level changes may occur, just as changes in age structure of plant populations and abundance of fungal species were identified only after six field seasons of treatments. Changes in the plant populations have significant consequences for ecosystem processes: For example, an increase in vascular plants in a Finnish peatland allowed more methane to be conducted to the peatland surface (Niemi *et al.*, 2002b). However, the trend reported here towards more prostrate, denser *Sphagnum* capitula under near-ambient UV-B (Chapter 2) may have the opposite effect on methane emission, and this is currently under investigation (Pancotto, unpublished data).

Excavation of *Tetroncium* rhizomes revealed that leaf-scars could be used to assess seasonal and annual growth of *Tetroncium*. A retrospective analysis revealed that rhizome elongation was reduced by UV-B over the six years of the experiment. A strong seasonal effect indicated that the relative reduction in growth under near-ambient UV-B occurred concurrently with periods of high UV-B, but not year round. This little-used method of growth analysis may have application for assessing the longer-term implications of climate change on peatlands, since rhizomes can be preserved in the peat for 40 years or more. Analysis of carbon isotopes from rings of the *Tetroncium* rhizome may also prove illuminating in identifying historical changes in the predominant

constraints on growth. An increase in the enzymatic pathways leading to synthesis of phenolic UV-B-absorbing compounds (Saranga *et al.*, 1999) would leave the residual carbon in structural tissue of the rhizome enriched in stable isotope ^{13}C. Thus, if an increase in the ^{13}C isotopic composition without a concurrent increase in rhizome growth were to occur, this would indicate reduced growth efficiency due to solar UV-B.

Overall fungal abundance was not significantly altered under near-ambient UV-B during the final three field seasons of treatments (Chapter 3). However, detailed analysis of the fungal community revealed species-specific changes in abundance. In particular, populations of some of the more common species increased under near-ambient UV-B, whilst other species declined (Chapter 3). This result illustrates the value of individual species analysis of the fungal community. Given that vertical penetration of radiation into the *Sphagnum* capitulum is very limited, it may not be surprising that those cultured fungal species inhibited by lamp UV-B did not always respond similarly (to near-ambient UV-B) in the peatland plots (Chapter 3).

The more compact *Sphagnum* capitula (Chapter 2) under near-ambient UV-B may help to explain the concurrent increase in testate amoebae (Chapter 4) and some fungal species (Chapter 3). The effect on testate amoebae was consistent throughout the study period (Searles *et al.*, 2001a), and supports the view that these micro-organisms respond quickly to environmental perturbations (Mitchell *et al.*, 2000). An increase in nutrient concentrations in the water held by the *Sphagnum* capitula may be attributable to increased leaching from the *Sphagnum* leaflets under near-ambient UV-B (Chapter 4). This would be consistent with the rise in acidity that also occurred under near-ambient UV-B (Chapter 3). Such an increase in available nutrients could lead to a bottom-up

trophic cascade. This would explain the growth of populations of some fungi and testate amoebae, but not the decrease in rotifers and nematodes (Chapter 4). The drop in rotifer and nematode populations was not apparent during the first three years of this study, and its cause is not immediately obvious. The trophic relationships between peatland micro-organisms are not clearly defined, and as our understanding of the ecosystem processes improves we should be able to better explain the changes reported.

The effects of UV-B on the *Sphagnum* peatland were more striking than those from a nearby *Carex* fen. Aboveground growth of *Carex* was unaffected by UV-B over five field seasons of treatments, but summer root growth and mycorrhizal colonization were reduced by near-ambient UV-B (Zaller *et al.*, 2002, 2004a). As with *Tetroncium* in the peatland, this suggests that while leaves adjust to UV-B, whole plant productivity is affected on a seasonal basis because of UV-B compensatory responses. Investigation of ecosystem-level responses to UV-B showed that slug diet selection shifted towards native herb *Gunnera magellanica*, away from *Nothofagus antarctica* (Zaller *et al.*, 2003). Although no effect on leaf C:N ratio was reported, this diet shift and changes to the decomposer community on *Gunnera* leaves grown under near-ambient UV-B (Pancotto *et al.*, 2003), suggest that UV-B did have an undetected effect on *Gunnera* leaf properties. The sensitivity of micro-organisms to subtle environmental changes resulting from UV-B treatment not immediately apparent in their host plants, is also supported by results from the peatland (Chapters 3 & 4). Other long term studies of an arctic heath, have reported soil bacterial and fungal communities to be altered, and soil C:N ratios to decrease, due to UV-B treatment (Johnson, 2003).

Both the UV-B received during growth and during decomposition influenced the fungi and bacteria present on decaying leaves of *Gunnera* (Pancotto *et al.*, 2003). The rate of early-stage decomposition of standard material was accelerated by UV-B, possibly due to photochemical degradation or changes in the decomposer fauna. This increase was partially negated by a decrease in later decomposition, thought to be attributable to reduced tissue quality under near-ambient UV-B (Pancotto *et al.*, 2004). These results are consistent with; a reduction in leaf nitrogen reported in *Tetroncium* under near-ambient UV-B (Chapter 2); and an increase in abundance of those fungi that are particularly active in the early stages of decomposition, such as, *Mortierella* and *Aureobasidium* (Chapter 3).

Context & Implications

The difference in mean daily UV-B flux between our treatments at the height of the field season was roughly 5 kJ m^{-2} day^{-1}, much less than the doses typically given in most UV-B supplementation studies (Searles *et al.*, 2001b; Flint *et al.*, 2003). Given that the effects of supplemental UV-B are usually quite modest, it is surprising that the low UV-B treatments in these investigations elicited so many measurable responses in the peatland ecosystem. Several authors have recently proposed that low doses of UV-B radiation may be important in activating physiological mechanisms at a baseline level (Paul, 2001; Aphalo, 2003; Paul & Gwynn-Jones, 2003). However, uncertainties remain about the mechanism of UV-B response. A specific pathway mediating UV- response has proved elusive, but recent research indicates that multiple molecular sensors act to increase reactive oxygen species in the cell, by activating a similar sequence of genes to those stimulated in insect damage or systemin elicitation responses (Balleré, 2003).

Meanwhile, research into UV-B effects at multiple trophic levels may provide the best indication of how continued ozone depletion influences ecosystems. Our understanding of ecosystems such as peatlands is not sufficient to predict how a change in plant growth or the microfaunal population may be reflected at other levels of organization within the ecosystem. Most of the effects of UV-B reported in this study have persisted through the six field seasons of treatments. Given their persistence, we can expect changes in the character of the ecosystem to occur over a longer period of time. Although our UV-B treatments were larger than the changes due to ozone depletion, our data can be used as a guideline for other ecosystem studies into the importance of ambient UV-B doses.

It is not yet understood how global climate change will affect peatland plant communities. Common bog plants such as *Sphagnum* and *Empetrum* are generally considered stress tolerant and somewhat unresponsive to environmental change (Shevtsova *et al.,* 1995; Gerdol, 1996; Press *et al.,* 1998; Tybirk *et al.,* 2000; Weltzin *et al.,* 2000). The differing responses of plants to rising atmospheric CO_2, increased nitrogen deposition, more intense UV-B and warmer temperatures, hinder our ability to synthesize a general pattern. Nitrogen deposition caused increased growth of vascular plants but not *Sphagnum* in northern and central European peatlands (Heijmans *et al.*, 2001; Mitchell *et al.*, 2002). Elevated CO_2 had the contrary effect, enabling *Sphagnum* to gain a competitive advantage over less responsive emergent vascular plants (Gehrke *et al.*, 1996; Heijmans *et al.,* 2001). Simulated warming only increased growth of *Sphagnum* (Gerdol *et al.*, 1998) or vascular plants (Hobbie *et al.,* 1999.) when other factors were not limiting. Increased precipitation in peat bogs usually leads to greater *Sphagnum*

dominance, whereas emergent vascular plants benefit from periods of drought (Bell & Tallis, 1974; Malmer *et al.* 1994). Pheonix *et al.* (2001) reported that supplemental watering simulating increased precipitation negated the effects of increase UV-B on plants in a Swedish heath system. Similarly during high precipitation years in Tierra del Fuego the response of *Tetroncium* to UV-B was least pronounced (Chapter 2).

Another pressing concern for the environment of Tierra del Fuego and the Antarctic peninsula is an incremental increase in mean annual temperature experienced over at least the last 100 years (Rosenbluth *et al.*, 1997; Strelin & Itturapse, 2003). Whilst many experiments have investigated the potential influence of global warming on Northern Hemisphere peatlands (Shaver *et al.*, 2000), the potential synergistic effects of warming and ozone depletion have been relatively unstudied (Day *et al.*, 1999; Zaller *et al.*, 2004b). High temporal variability in response to UV-B was evident in this study. This variability and other predicted global environmental changes, such as more variable moisture availability and net radiation, may mitigate the influence of UV-B. On a global scale, the peatlands of Tierra del Fuego also offer a unique contrast with Northern Hemisphere peatlands that are subject to increased N deposition due to atmospheric pollution (Perakis & Hedin, 2001). As such, the continued study of Tierra del Fuego peatlands would help to give a global perspective on peatland function and adaptability to climate change.

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APPENDICES

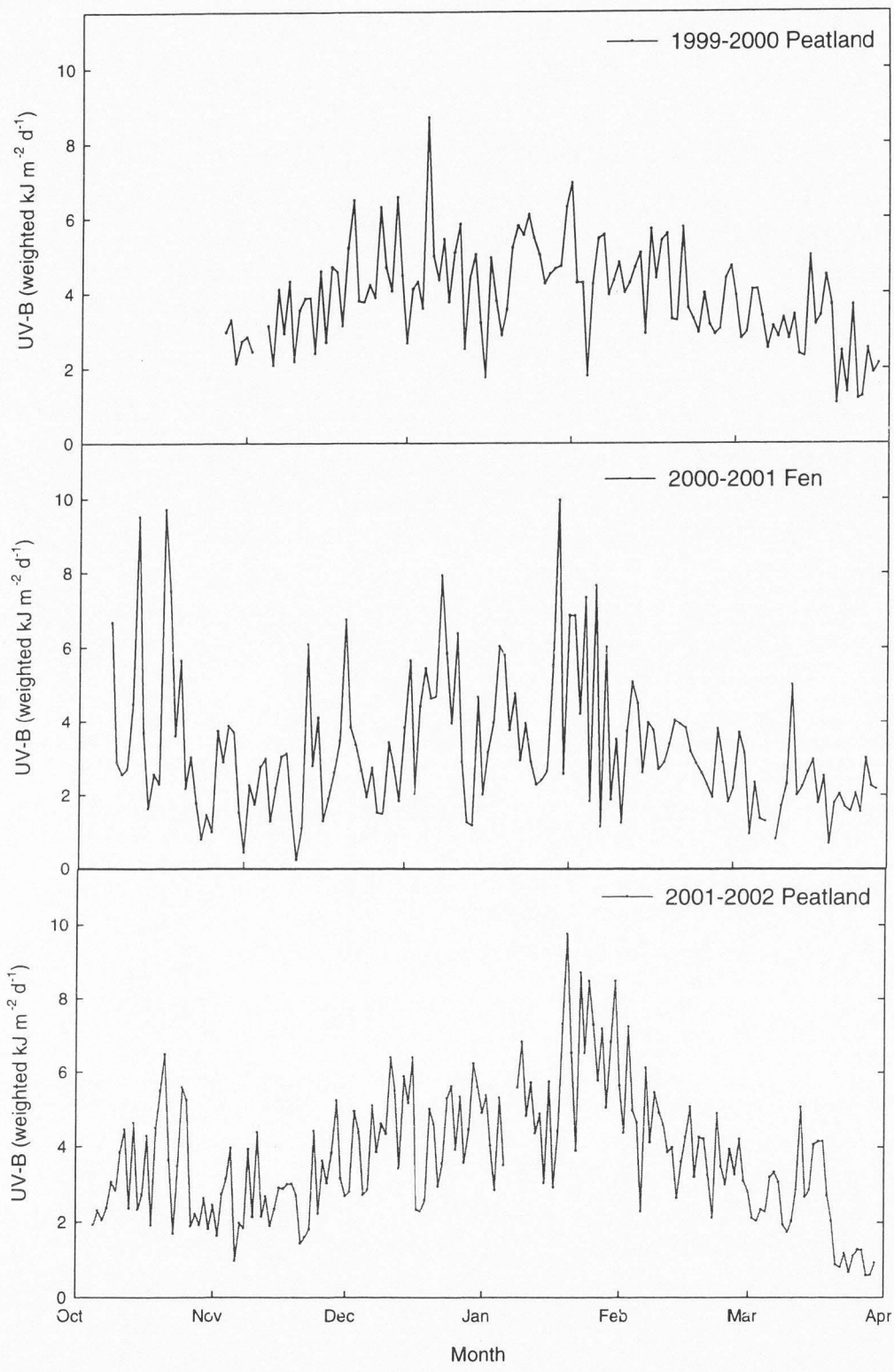
APPENDIX A

UV-B RADIATION AND METEOROLOGICAL DATA

Fig. A.1 Measured values of integrated daily solar UV-B radiation (normalized to one at 300 nm and weighted with the generalized plant action spectrum) from October to March. The daily solar UV-B monitored using a broadband global radiation sensor (Solar Light Co., Model PMA2102, Philadelphia, Pennsylvania, USA) is shown for each of the three growing seasons. Data were recorded every fifteen minutes by a Campbell Scientific 21x datalogger (Logan, Utah, USA). Gaps in the data correspond to periods of time when the datalogger was broken. Accuracy of the UV-B data was established by comparison with data from the NSF UV-B monitoring station in Ushuaia SUV-100 spectroradiometer (courtesy of S Díaz).

Meteorological data were recorded at the peatland site during the 1999-2000 and 2001-2002 field seasons. During the 2000-2001 field season only meteorological data from our fen field site, in Andorra valley to the east of Ushuaia, are available because of problems with our datalogger at the peatland.

The Antarctica ozone holes of 1999, 2000 and 2001, were three of largest to occur. The pattern of ozone depletion and recuperation occurred slightly earlier during these years than in previous years. Consequently large daily changes in the total UV-B radiation received over Tierra del Fuego occurred on a few days during October and November when depleted air from the ozone hole passed overhead. However, ozone depletion was less influential later in the growing season (December) compared to previous years.


1999-2000 Peatland
2000-2001 Fen
2001-2002 Peatland
UV-B (weighted kJ m-2 d-1)
0
2
4
6
8
10
Oct
Nov
Dec
Jan
Feb
Mar
Apr
Month

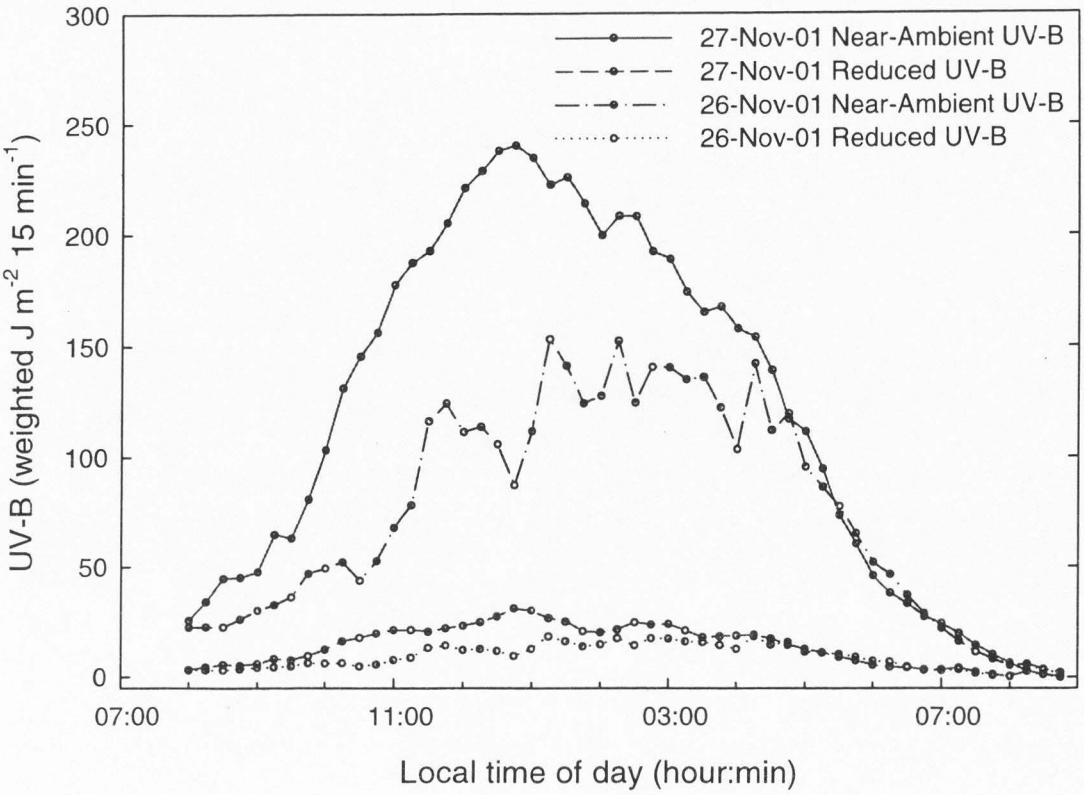


Fig. A.2 Daily patterns of UV-B on two typical days in the austral spring, measured in peatland near-ambient UV-B (c. 90% of ambient) and reduced UV-B (17% of ambient) plots. UV-B radiation (normalized to one at 300 nm and weighted with the generalized plant action spectrum, see Fig. A-1) is integrated over 15-minute periods.

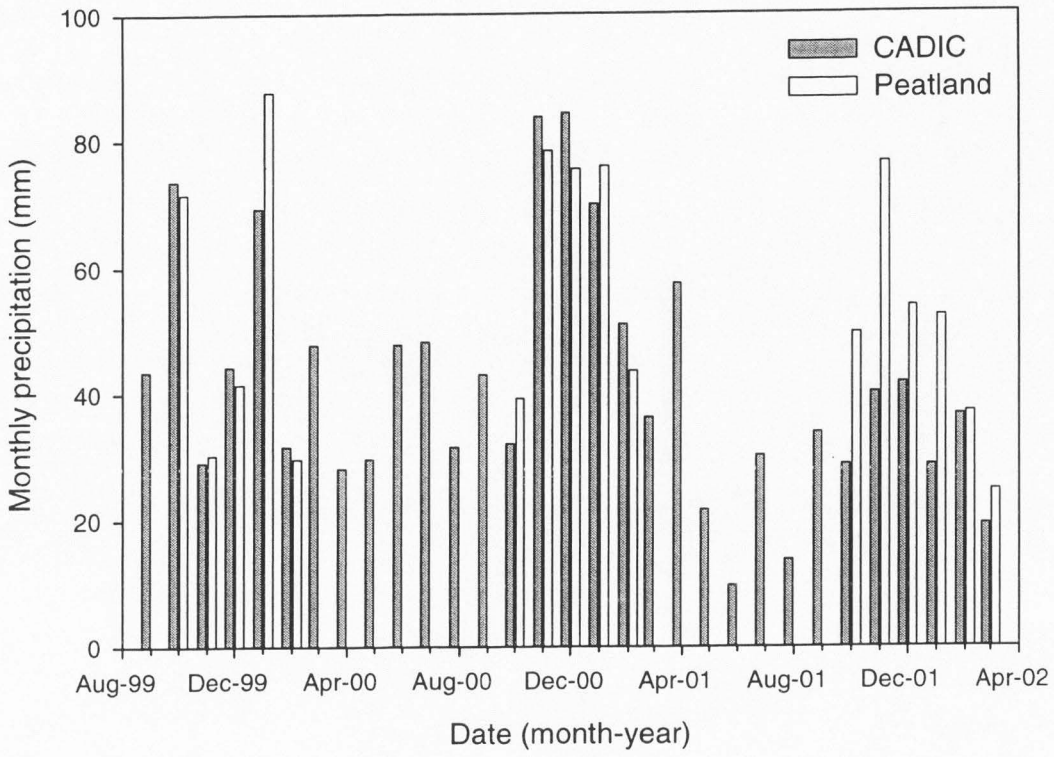


Fig. A.3 Total monthly precipitation measured at the peatland site during the growing season (October – February) manually using a rain gauge and by "Rain Collector II" (Davis instruments, Hayward, California, USA) as part of our meteorological station (see Fig. A.1). This is compared with precipitation recorded by the CADIC meteorological station in Ushuaia throughout the year (courtesy of R Itturaspe). Whole year data from Ushuaia corresponded closely with data from the peatland. They show that most of the annual precipitation during each year fell in spring and early summer, and that 2000 was a particularly wet year.

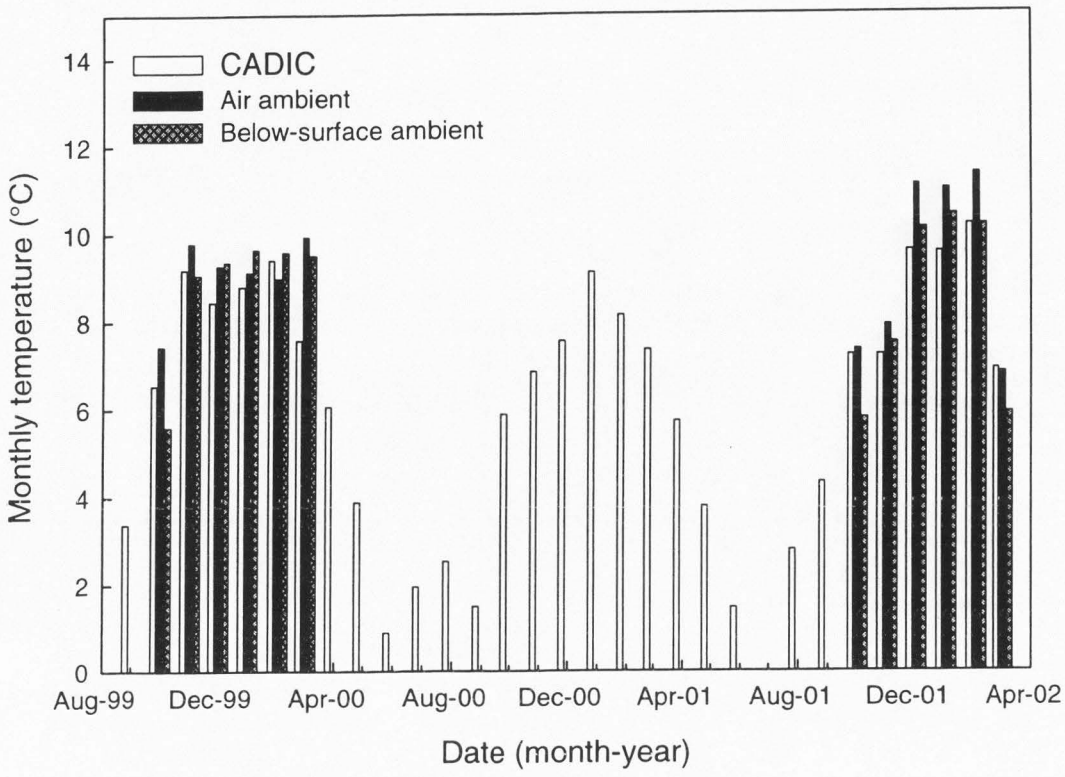


Fig. A.4 Mean monthly temperature measured at the peatland site during the growing season (October – March). Eight custom-made thermisters (C. Ashurst, USU) located in several sample plots, were attached to our meteorological station (see Fig. A.1). These data are compared with monthly temperature recorded by the CADIC meteorological station, in Ushuaia, throughout the year (courtesy of R Itturaspe).

Monthly spring and summer temperatures at the study site were similar and data from Ushuaia. Despite being covered by snow for most of the winter, the mean monthly temperature was below zero for just one month of the year, reflecting the oceanic climate.

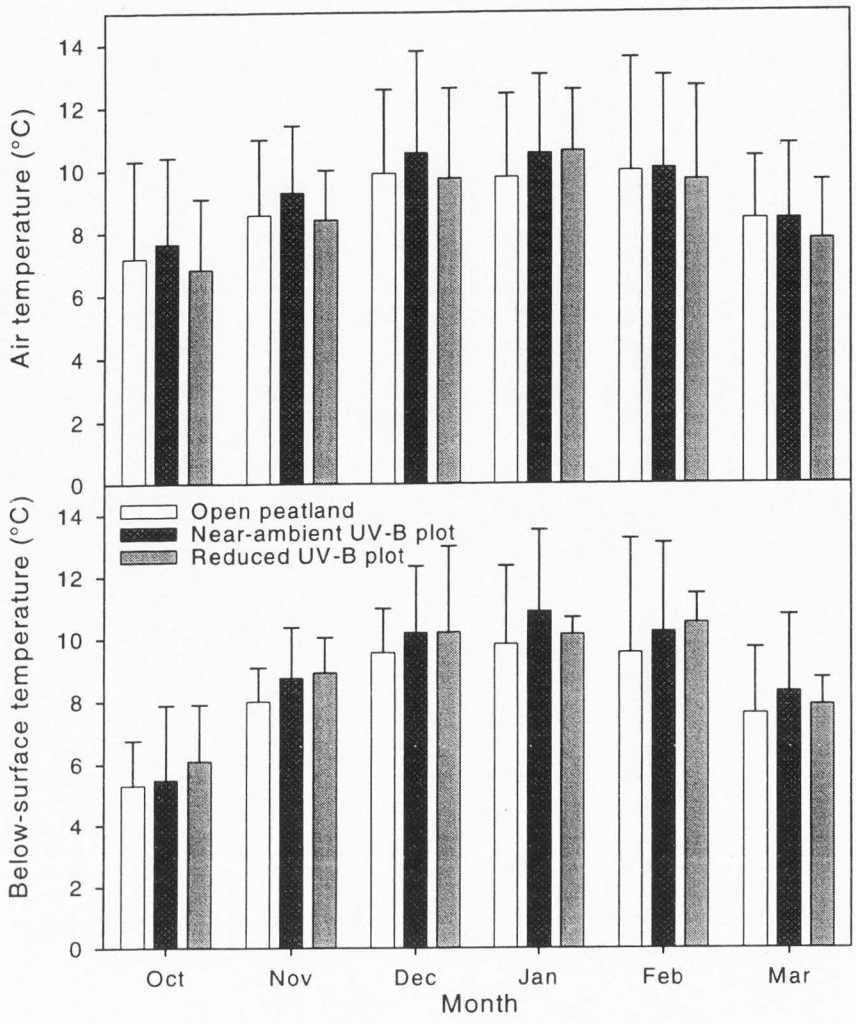


Fig. A.5 Temperature above and below the peatland surface inside the near-ambient UV-B plots, the reduced UV-B plots, and in the open peatland. Average daily temperature for each month during the 1999-2000 and 2001-2002 field seasons + 1 standard deviation. The mean temperature under the filter was slightly higher, and the temperature range greater (data not shown), but this difference was small (October-February mean, +0·2° C air temp, +0·4° C soil temp), and similar between the two filter types. Below-surface temperature remained a few degrees lower than air temperature during spring, but during January and February, air and below-surface temperatures were comparable.

Table A.1 Wind speed at the peatland 2001-2002 (m sec^{-1}: average over 15 minutes). Measured with an anemometer (Davis instruments, Hayward, California, USA), attached to our meteorological station (see Fig. A.1).

Month	Mean		Maximum	
	50 cm height	20 cm height	50 cm height	20 cm height
Oct	2.23	0.99	7.55	4.00
Nov	2.11	0.96	7.71	4.29
Dec	2.22	1.11	7.10	3.94
Jan	1.88	0.89	6.52	4.13
Average	2.11	0.99	7.22	4.09

APPENDIX B

SUPPLEMENTAL INFORMATION AND DATA

Empetrum Germination trial

A growth chamber germination trial of seed collected from under the two UV-B treatments was carried out in Logan (July, 2000). Seeds were subjected to a variety of pre-sewing treatments to try and enhance germination, such as cold chilling, changes in photoperiod, and various methods of seed-coat abrasion. Percentage germination of *Empetrum* was too low to confidently determine the effect of UV-B. Of the various treatments administered, only the combination of sand-papering of the seed coat and application of gibberellic acid gave significantly increased germination at 5° C.

Insect herbivory on *Tetroncium* and *Nothofagus*

The number of leaves of *Tetroncium* dissected by leaf cutting insects in spring, or grazed by geese in summer. , was not affected by UV-B treatment. Neither was there a treatment effect on the presence of stem-feeding aphids on each of the measured branches of *Nothofagus* at the time of leaf expansion. Any change would be important, as branches with sap sucking aphid colonies tended to die in the following year.

Table B.1: a) Fecundity of peatland *Sphagnum, Tetroncium,* and *Empetrum*. **b)** Seed properties of *Empetrum* and *Tetroncium*. *Tetroncium* male and female flower spikes and seeds were recorded each February (1999-2002). *Empetrum* berry production was measured every year in January when berry abundance was judged to be highest, but considerable herbivory and the non-synchronous production of berries made total berry production difficult to compare between years. *Sphagnum* sporulation was infrequent and patchy, consequently data were not assessed statically. Seeds sampled during the 2000-2001 field season were separated and weighted.

a)	1999-2000	2000-2001	2001-2002	UV-B	Year	UV × Year
Empetrum fruits (# plot^{-1})						
Near-ambient UV-B	1.7 ± 1.0	13.4 ± 3.7	15.6 ± 5.1	0.027	0.004	0.106
Reduced UV-B	14.8 ± 9.0	45.7 ± 14.2	23.5 ± 6.4			
Male *Tetroncium* flowers (# plot^{-1})						
Near-ambient UV-B	12.0 ± 6.3	8.2 ± 4.8	6.3 ± 3.5	0.644	0.041	0.472
Reduced UV-B	8.9 ± 3.9	4.0 ± 2.4	0.8 ± 0.4			
Female *Tetroncium* flowers (# plot^{-1})						
Near-ambient UV-B	3.4 ± 0.9	4.8 ± 1.0	2.5 ± 1.6	0.093	0.018	0.003
Reduced UV-B	16.8 ± 4.9	16.6 ± 6.0	4.5 ± 1.9			
Tetroncium Seeds (# plot^{-1})						
Near-ambient UV-B	6.2 ± 3.6	14.6 ± 3.6		0.002		
Reduced UV-B	50.6 ± 11.6	43.2 ± 15.0				
Sphagnum capsules (# plot^{-1})						
Near-ambient UV-B			1.9 ± 1.7			
Reduced UV-B			10 ± 6.7			

Means ± 1 SE of 10 plots of each UV-B treatment. *P* values from a mixed model ANOVA.

b) *Tetroncium* seeds	Seed heads (# plot^{-1})	Mass (mg seed^{-1})	Seeds (# flower^{-1})
Near-ambient UV-B	24.3 ± 10.9	410 ± 30	23.48 ± 3.80
Reduced UV-B	110.5 ± 23.6	440 ± 30	22.83 ± 2.85
P value	0.004	0.513	0.744
Empetrum seeds			
Near-ambient UV-B		71.1 ± 6.2	
Reduced UV-B		77.0 ± 6.3	
P value		0.534	

Means ± 1 SE of 10 plots of each UV-B treatment. *P* values from a single factor ANOVA

The reduction in fecundity of *Tetroncium* (fewer female flowers and seeds) and *Empetrum* (equal flowers, but fewer berries) under near-ambient UV-B are unusual results. Previous research has reported no affect of supplemental UV-B on the abundance of *Empetrum* fruits in a subarctic heath (Gwynn-Jones *et al.,* 1997; Pheonix *et al.,* 2001; for full references see Chapter 2). Given that most *Empetrum* and *Tetroncium* in the peatland are produced asexually, the peatland community composition is unlikely to be affected by these changes. Also, since fecundity prior to implementation of the treatments was not assessed these results can not be considered definitive. Further research is needed to assess whether changes in berry production are caused by reduced pollination or a lower proportion of fruits set.

Table B.2 Annual root production and rhizome division of *Tetroncium*.

Root production and division was assessed retrospectively from rhizomes taken from the peatland. Annual rhizome elongation was determined as the distance between tightly clustered leaf scars produced in the autumn of each year.

Field Season	2002-2001	2001-2000	2000-1999	1999-1998	1998-1997	1997-1996
# Roots	7.1 ± 0.7	7.5 ± 0.6	5.3 ± 0.6	3.6 ± 0.4	3.1 ± 0.5	1.9 ± 0.5
	7.2 ± 0.4	6.8 ± 0.5	5.5 ± 0.6	4.4 ± 0.6	4.3 ± 0.5	1.8 ± 0.5
P value	0.94	0.95	0.36	0.82	0.22	0.07
# Divisions	1.0 ± 0.2	0.7 ± 0.2	1.1 ± 0.3	0.9 ± 0.2	0.4 ± 0.1	0.2 ± 0.1
	0.9 ± 0.2	1.0 ± 0.3	0.9 ± 0.3	0.9 ± 0.2	0.2 ± 0.1	0.4 ± 0.2
P value	0.78	0.75	0.41	0.39	1.00	0.02

Means ± 1 SE of 10 plots of each UV-B treatment. *P* values from single factor ANOVA.

Table B.3 *Tetroncium magellanicum* leaf production and growth

Data were recorded during February each field season. Brown leaves from only the current field season were counted. Single factor ANOVA was used to calculate individual *P* values are given for each field season. Repeated measures mixed model ANOVA (Chapter 2) was used to calculate *P* value given at the end of each row.

Tetroncium leaf Treatment	Field Season (FS) 1999-2000	2000-2001	2001-2002	Repeated measure	*P* value
Number of Green leaves					
Near-ambient UV-B	3.45 +/- 0.11	3.32 +/- 0.10	3.45 +/- 0.08	UV-B	0.409
Reduced UV-B	3.36 +/- 0.06	3.20 +/- 0.05	3.48 +/- 0.07	FS	< 0.001
P value	0.379	0.253	0.621	UV-B*FS	0.247
Number of Brown leaves					
Near-ambient UV-B	1.20 +/- 0.10	0.76 +/- 0.09	0.42 +/- 0.08	UV-B	0.081
Reduced UV-B	1.26 +/- 0.09	1.00 +/- 0.15	0.59 +/- 0.05	FS	< 0.001
P value	0.459	0.242	0.122	UV-B*FS	0.496
Largest leaf in February					
Near-ambient UV-B	37.9 +/- 3.0	48.4 +/- 3.0	48.1 +/- 3.6	UV-B	0.089
Reduced UV-B	39.86 +/- 2.1	52.1 +/- 2.1	51.8 +/- 2.7	FS	< 0.001
P value	0.349	0.045	0.311	UV-B*FS	0.497
2nd Largest leaf in February					
Near-ambient UV-B	26.8 +/- 1.7	42.1 +/- 2.6		UV-B	0.211
Reduced UV-B	31.7 +/- 1.6	45.1 +/- 1.7		FS	< 0.001
P value	0.005	0.176		UV-B*FS	0.084

Means ± 1 SE of 10 plots of each UV-B treatment.

Table B.4 Fungal colonisation of *Tetroncium* leaves

Dark circular colonies of *Cladosporium* on brown senesced leaves of 16 *Tetroncium* plants per plot were counted in October of 2001.

UV-B Treatment	Length (mm)	dry mass (mg)	Side 1 # Colonies	Side 1 % Cover	Side 2 # Colonies	Side 2 % Cover
Near-ambient UV-B	3.7 ± 0.3	52 ± 6	17.61 ± 2.26	36.6 ± 5.2	16.54 ± 2.04	34.7 ± 4.9
Reduced UV-B	4.1 ± 0.2	61 ± 9	16.5 ± 2.03	32.1 ± 3.8	15.78 ± 1.97	30.4 ± 3.5
P value	0.029	0.113	0.642	0.507	0.735	0.485

Mean ± 1 SE of 10 plots of each UV-B treatment. *P* value from single factor ANOVA

Table B.5 Abundance of minor microfauna during the final field season (2001-2002).

Microfauna included are testate amoebae, non-testate protozoa, and a testate Rotifer. Three sample month means are pooled.

Species	0-5 mm Depth		5-10 mm Depth		*P* value	
UV-B Treatment	Near-Ambient	Reduced	Near-Ambient	Reduced	UV	UV × Depth
Assulina semilunum	14.1 ± 1.5	7.3 ± 0.9	26.5 ± 2.6	11.6 ± 1.2	0.092	0.452
Centropyxis aerophila	0.8 ± 0.1	0.7 ± 0.1	0.04 ± 0.02	0.05 ± 0.02	0.752	0.681
Corythion dubium	15.0 ± 0.9	16.8 ± 1.8	4.0 ± 0.6	8.5 ± 1.0	0.461	0.389
Difflugia oblonga	47.8 ± 3.4	50.1 ± 3.6	21.8 ± 2.2	35.8 ± 4.0	0.600	0.378
Euglypha sp2	4.4 ± 0.7	2.1 ± 0.4	2.4 ± 0.3	2.0 ± 0.5	0.388	0.519
Centropyxis arcelloides type	11.0 ± 0.9	5.7 ± 0.9	14.7 ± 1.5	13.3 ± 1.4	0.261	0.382
Small *Nebula*	7.8 ± 0.8	18.6 ± 2.0	6.5 ± 0.8	11.4 ± 1.2	0.330	0.424
Heleopera petroicola	22.5 ± 2.2	17.6 ± 1.9	30.6 ± 3.4	26.4 ± 2.6	0.449	0.879
Heleopera silvatica	0.11 ± 0.0	0.3 ± 0.1	2.5 ± 0.4	0.7 ± 0.1	0.336	0.106
Hyaloshena sp	9.9 ± 0.8	3.6 ± 0.5	4.6 ± 0.7	8.0 ± 1.1	0.355	0.014
Nebula sp.	0.1	0	0.1	0	0.166	0.354
Naked *Protozoa*	45.3 ± 3.0	43.3 ± 3.1	9.3 ± 0.9	19.1 ± 1.9	0.369	0.090
Testate *Rotifera*	0.1 ± 0.0	0.2 ± 0.1	0.1 ± 0.0	0.3 ± 0.1	0.424	0.849

Data are back-transformed means ± 1 SE. UV-$B_{1,9}$ UV*$Depth_{11,8}$. *P* values from mixed model ANOVA.

Table B.6 Fungal species growth rates under supplemental UV-B radiation.

Species	Phenolics		Glucose enriched	
	Colony growth rate (mm hour^{-1})	*P* value	Colony growth rate (mm hour^{-1})	*P* value
Mortierella alpina	0	0.002	0.453	0.461
Penicillium thomii	0.372	0.478	0.469	0.332
Mucor hiemalis	0.330	0.050	1.141	0.943
Mortierella vinacea	0	0.005	0.286	0.060
Penicillium frequentans	0.292	0.047	0.479	1.000
Aureobasidium sp	0.172	0.002	0.468	0.189
Aspergillus sp	0.292	0.319	0.323	0.393
Cladosporium herbarum	0.096	0.017	0.167	0.419

Colony growth rate per hour was calculated by linear regression of colony diameter over 6 days (All R^2 >0.90). *P* values from mixed model ANOVA ($N = 4$).

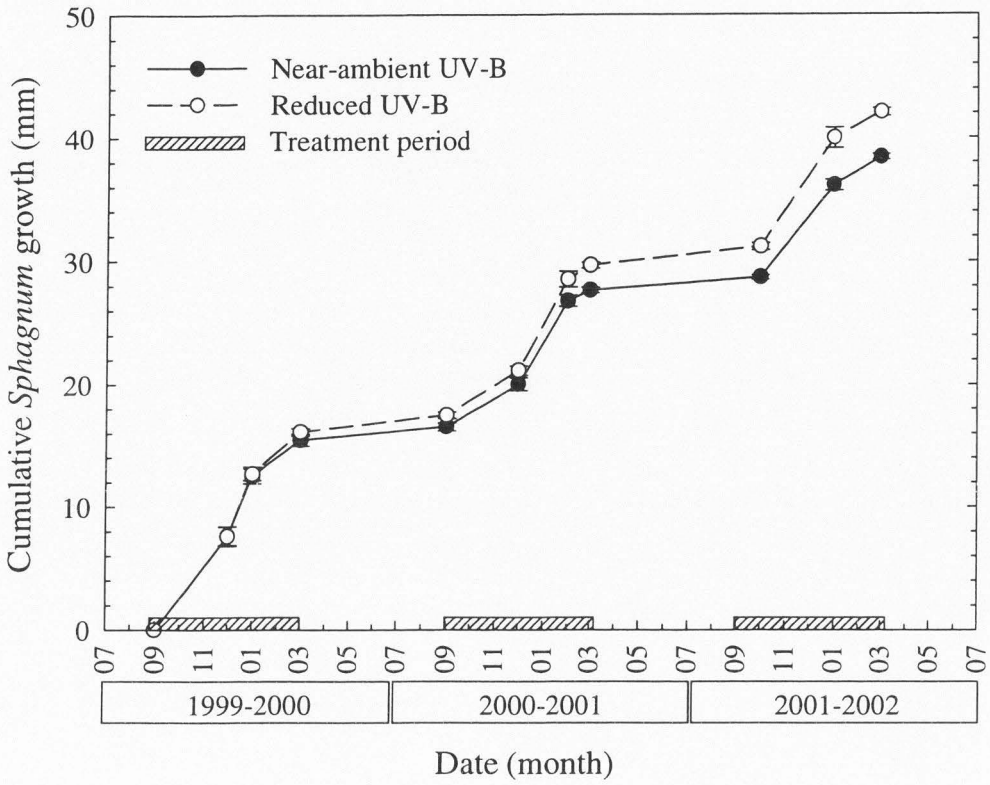


Fig. B.1 Cumulative *Sphagnum magellanicum* height growth during the three seasons of experimentation (1999-2002).

Mean of 10 plots under each UV-B treatment ± 1 SE. The striped block represents the period of time when the filters were in place. Yearly total reduction with near-ambient UV-B was; 5.0% 1999-2000; 10.1% 2000-2001; 13.1% 2001-2002. The cumulative difference between treatments was significant ($P = 0.037$), but individual field seasons were not. Repeated measures analysis give a significant effect of UV-B on growth in the spring ($P = 0.035$) and summer ($P = 0.028$), and significant variability between years ($P < 0.001$).

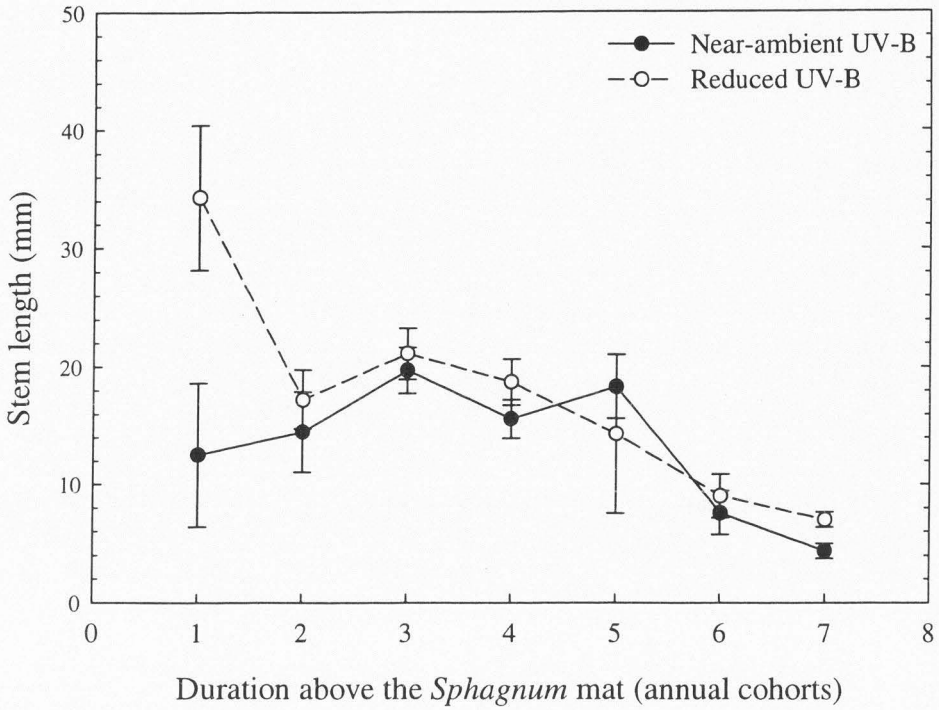


Fig. B.2 New *Empetrum* stem growth for cohorts of stems classified by number of years of growth above the *Sphagnum* mat.

Mean ± 1 SE of all plants sampled from 10 plots of each UV-B treatment. Growth was calculated from plants harvested during February, 2000 & 2002. New growth declined with duration above the *Sphagnum*, allowing the *Sphagnum* mat to engulf older stems.

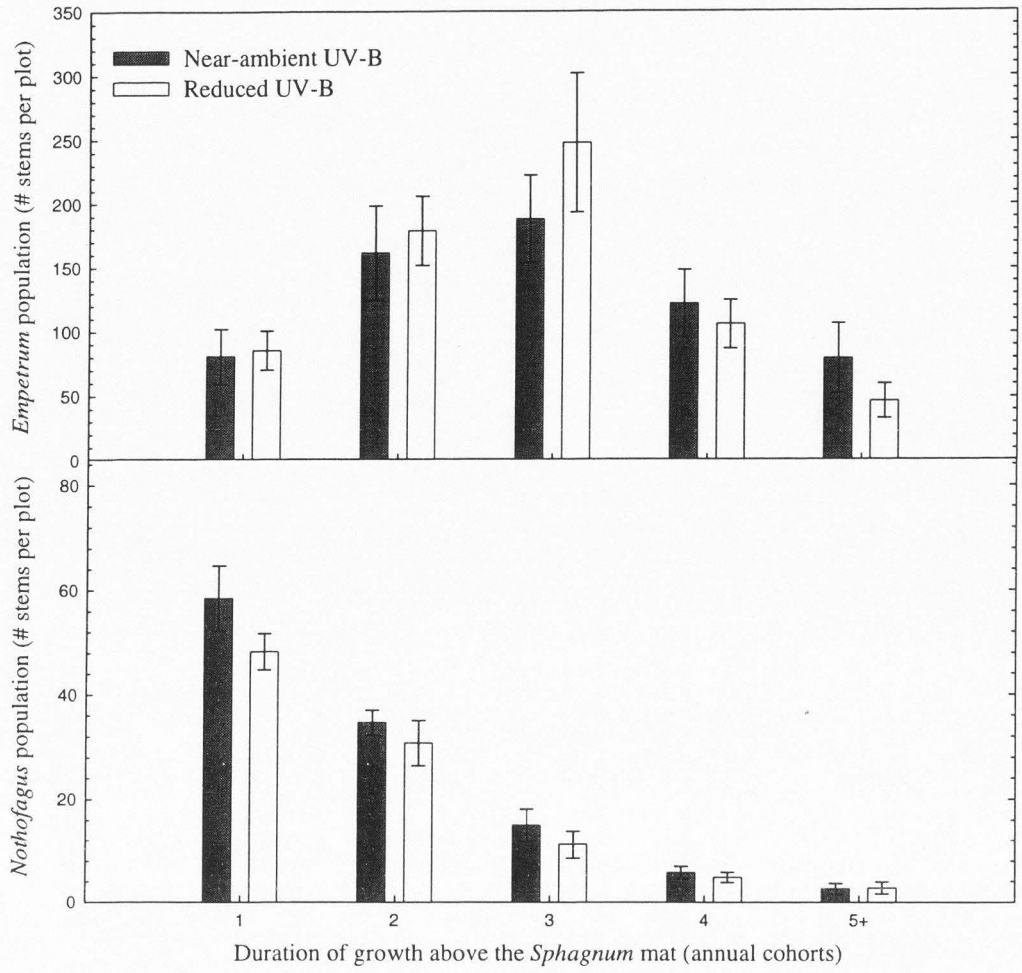


Fig. B.3 Mean population size of *Empetrum* and *Nothofagus* over two field-seasons (2000-2002) under near-ambient UV-B and reduced UV-B.

Mean ± 1 SE of 10 plots of each UV-B treatment. A 120-×-60-cm area was cencussed at the end of each field season. UV-B treatment did not significantly affect the total *Empetrum* population or apparent age structure, or the total population of *Nothofagus* stems. Significantly more *Nothofagus* stems with two years of growth above the *Sphagnum* mat were present under near-ambient UV-B than under reduced UV-B ($P = 0.054$). There was a similar tendency (NS) in *Nothofagus* stems with one and three years of growth above the *Sphagnum* mat.

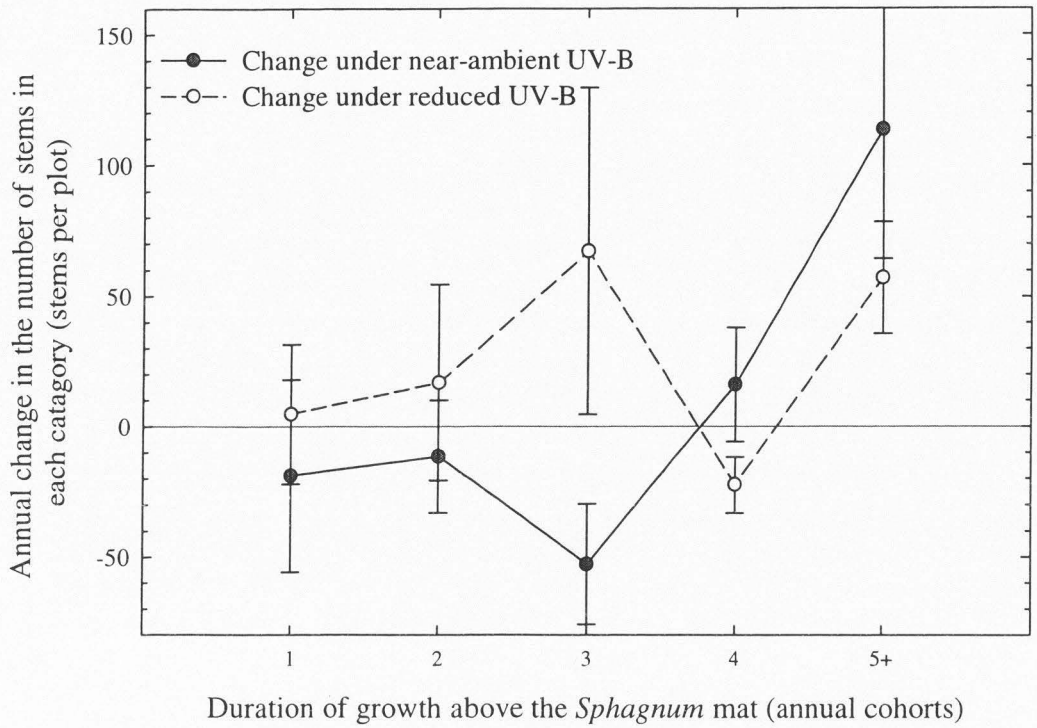


Fig. B.4 Change in *Empetrum* population over two field seasons (2000-2002). Mean ± 1 SE of 10 plots under each UV-B treatment. The zero line represents no change, negative numbers indicate fewer stems, and positive values - more stems. There was a marginally significant decrease in *Empetrum* stems with two (P; 0.05-0.10) and three ($P < 0.05$) years of growth above the *Sphagnum* mat under near-ambient, relative to reduced UV-B, and a similar increase in plants with four years of growth.

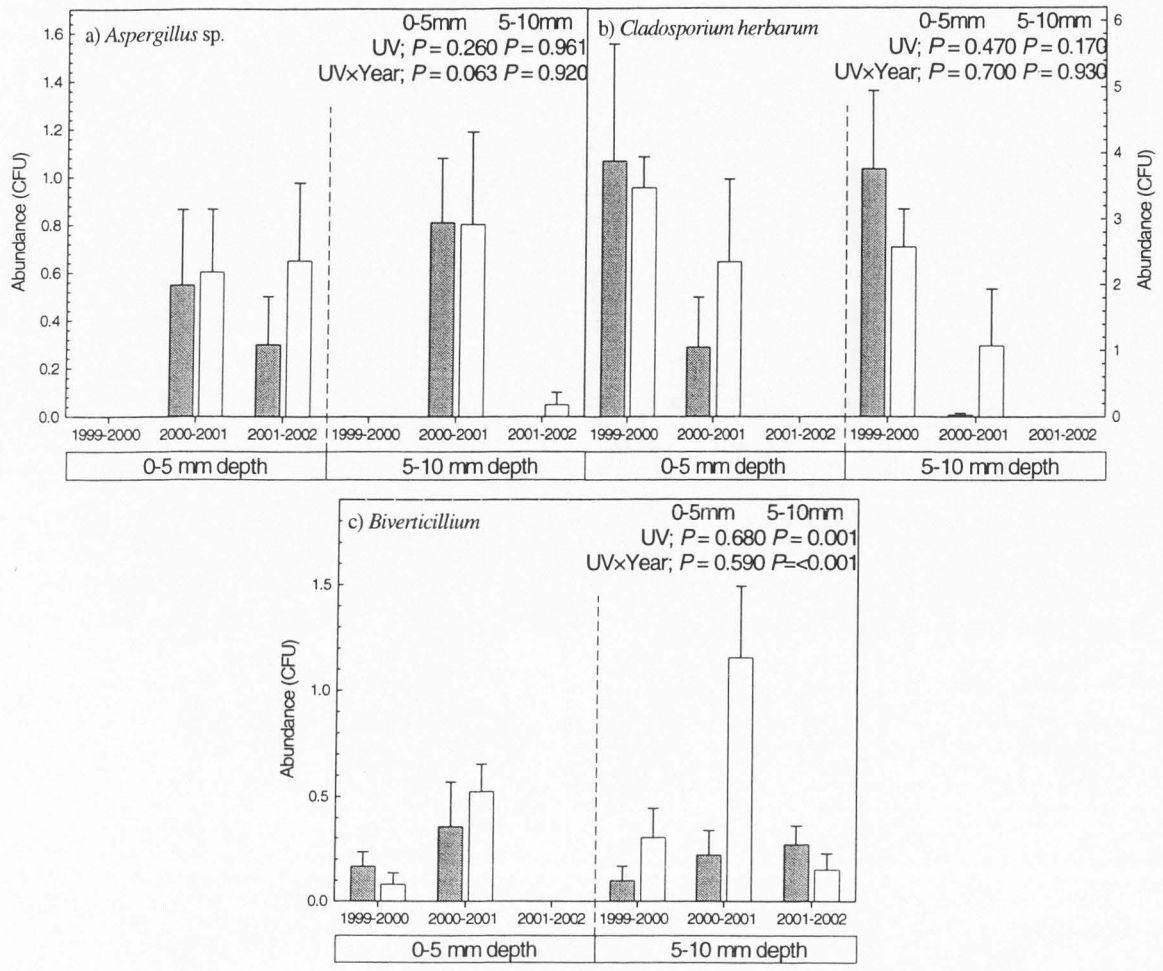


Fig. B.5 Abundance of individual fungal species from the peatland microfungal community under near-ambient and reduced UV-B. a) *Aspergillus* sp; b) *Cladosporium herbarum*; c) *Biverticillum.*

The number of CFU per 200 µl from each 6-ml sample containing 14 Sphagnum capitula is shown. Back-transformed means + 1 SE of multiple samples (3-4 occasions) for each field season.

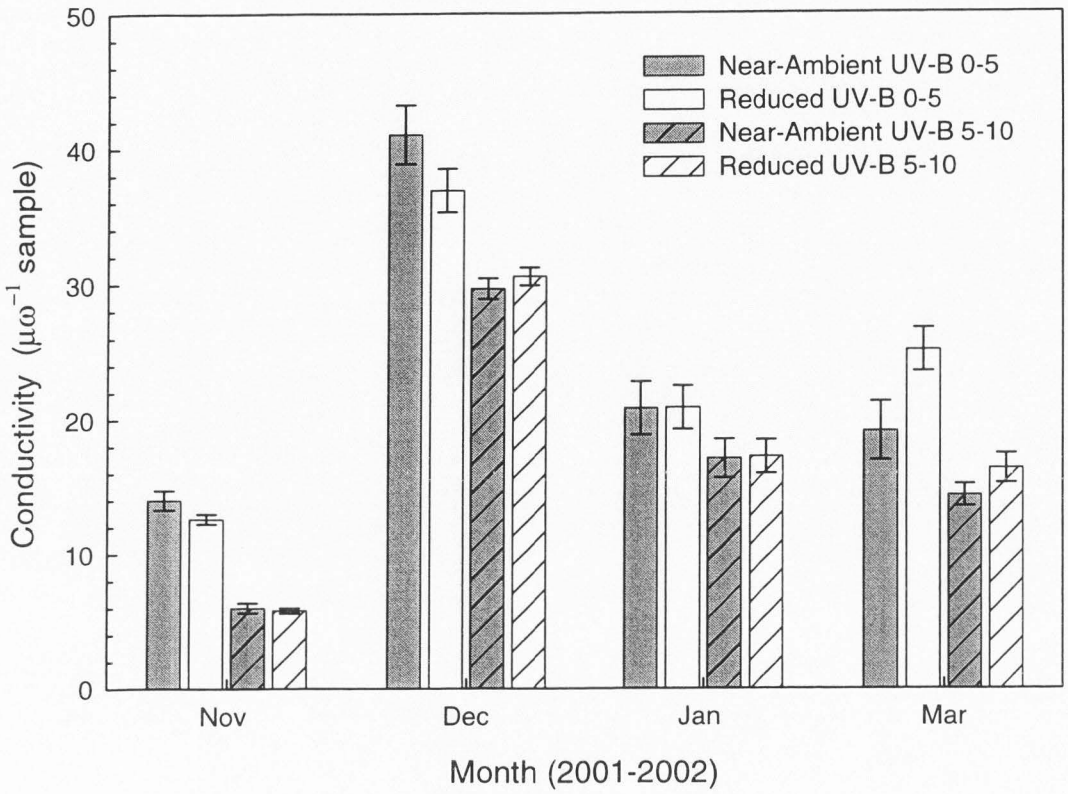


Fig B.6 Ionic concentration of water from the *Sphagnum* capitulum 24 hours after harvest. Monthly mean, 2001-2002 field season ± 1 SE:

APPENDIX C

LETTERS

IFEVA - Instituto de Investigaciones
Fisiológicas y Ecológicas Vinculadas a la Agricultura
CONICET y Universidad de Buenos Aires
Av. San Martín 4453
C1417 DSE, Buenos Aires, ARGENTINA
Tel.: 11 4524 8070 x8101
Fax: 11 4514 8730
ballare@ifeva.edu.ar

Mr. Matt Robson

Ecophysiology Group - Utah State University UV-B Project

E-mail: slbln@cc.usu.edu

Tel: 435-797-0194

Fax: 435-797-3872

Dear Matt,

As a co-author, I am pleased to give you my consent to publish the following papers as chapters in your dissertation:

Six years of solar UV-B manipulations affect growth of *Sphagnum* and vascular plants in a Tierra del Fuego peatland. *New Phytologist* (2003) 160: 379-389.

Solar UV-B treatments mediate changes in the *Sphagnum* capitulum microenvironment and the peatland microfungal community. Submitted to *Oecologia*

Solar UV-B influences microfaunal community composition in a Tierra del Fuego peatland. For submission to *Global Change Biology*.

Best wishes,

Carlos L. Ballaré
Associate Professor

Utah State
UNIVERSITY
The Ecology Center and
Department of Forest, Range, and Wildlife Sciences
5205 Old Main Hill, Utah State University,
Logan, Utah 84322-5205, USA

27th February 2004

Dear Matt:

As a co-author, I am pleased to give you my consent to publish the following paper as a chapter in your dissertation:

Six years of solar UV-B manipulations affect growth of *Sphagnum* and vascular plants in a Tierra del Fuego peatland. *New Phytologist* (2003) 160: 379-389.

Yours sincerely,

Stephan Flint
Research Associate

IFEVA
FACULTAD DE AGRONOMIA
UNIVERSIDAD DE BUENOS AIRES

Av. San Martin 4453, (1417) Buenos Aires, Argentina
Tel. (54 11) 4524 8070/71 Fax (54 11) 4 514 8730

Mr Matt Robson
Ecophysiology Group – Utah State University UV-B Project
E-mail: slbfn@cc.usu.edu
Fax: 435-797-3872

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Solar UV-B influences microfaunal community composition in a Tierra del Fuego peatland. For submission to *Global Change Biology*.

Sincerely,

Ana L Scopel
Adjunct Professor
e-mail: scopel@ifeva.edu.ar

Ushuaia, March 4th 2004

Dear Thomas Matthew Robson,

As a co-author, I am pleased to give you my consent to publish the following papers as chapters in your dissertation:

Six years of solar UV-B manipulations affect growth of *Sphagnum* and vascular plants in a Tierra del Fuego peatland. *New Phytologist* (2003) 160: 379-389.

Solar UV-B treatments mediate changes in the *Sphagnum* capitulum microenvironment and the peatland microfungal community. Submitted to *Oecologia*

Solar UV-B influences microfaunal community composition in a Tierra del Fuego peatland. For submission to *Global Change Biology*.

Verónica A. Pancotto

UNIVERSIDAD DE BUENOS AIRES
Facultad de Agronomía
Cátedra de Ecología
Av. San Martín 4453, (C1417DSE) Buenos Aires, Argentina
Tel. (54 11) 4524-8070 ext 8119 Fax: 4514-8730. E-mail: sala@ifeva.edu.ar

4 March 2004

Matt Robson
Ecophysiology Group –
Utah State University
Logan, UT

Dear Matt,

As a co-author, I am pleased to give you my consent to publish the following papers as chapters in your dissertation:

Six years of solar UV-B manipulations affect growth of *Sphagnum* and vascular plants in a Tierra del Fuego peatland. *New Phytologist* (2003) 160: 379-389.

Solar UV-B treatments mediate changes in the *Sphagnum* capitulum microenvironment and the peatland microfungal community. Submitted to *Oecologia*

Solar UV-B influences microfaunal community composition in a Tierra del Fuego peatland. For submission to *Global Change Biology*.

Sincerely,

Osvaldo Sala
Professor

CURRICULUM VITAE

Thomas Matthew Robson

The Ecology Center, Utah State University, 5205 Old Main Hill,
Logan, 84322, USA.
Website: www.cnr.usu.edu/research/projectUV
Nationality: British

Education

B Sc (Hons) Dunelm 1993-1996, in Biological Sciences (2:1) – University of Durham, UK (Phil Hulme).
M Sc 1996-1998, in Forest Science – University of Edinburgh, UK (John Grace; Pedro J Aphalo).
Ph D 1999-2004, in Ecology – Utah State University, Logan, USA (Martyn M Caldwell).

Post Doctoral Research

Commencing May 2004, Ecosystem Ecologist - Laboratoire d'Ecologie Alpine, CNRS, Université Joseph Fourier, BP 53, 38041 Grenoble Cedex 9, France.

Professional Employment

Internships: 1) Crop Research Technician at the Royal Agricultural College, Cirencester, UK; 2) Arboretum Superintendent, at Westonbirt Arboretum, Tetbury, UK.

Collaborators

Aphalo P.J. (University of Jyväskylä); Ballaré C.L. (Universidad de Buenos Aires); Brancaleoni L. (Universita di Ferrera); Cabello M. (Spegazzini-UNLP Argentina); Díaz S.B. (CADIC Argentina); Flint S.D. (Utah State University); Giordano C.V. (Universidad de Buenos Aires); Leffler A.J. (Louisiana Tech University); Pancotto V.A. (Universidad de Buenos Aires); Peek M.S. (Utah State University); Rousseaux M.C. (CRILAR La Rioja Argentina); Ryel R.J. (Utah State University); Sala O.E. (Universidad de Buenos Aires); Scopel A.L. (Universidad de Buenos Aires); Searles P.S. (CRILAR La Rioja Argentina); Zaller J.G. (University of Bonn).

Conferences

Environmental effects of ozone depletion and its interactions with climate change: 2002 assessment. UNEP meeting. *Park City, Utah, 13-19 September 2002.*

Conservacion de ecosistemas a nivel mundial con enfasis en las turberas de Tierra del Fuego. International field course / workshop. *Ushuaia, Argentina, 6-10 March 2000.* (Coronato A., Roig C.)

The Radiological consequences of the Chernobyl accident - EU conference. *Minsk, Belarus. 18-22 March 1996.*

Publications

Ballaré C.L.; Rousseaux M.C.; Searles P.S.; Zaller J.G.; Giordano C.V.; Robson T.M.; Caldwell M.M.; Sala S.E.; Scopel A.L. (2001) Impacts of solar ultraviolet-B radiation on terrestrial ecosystems of Tierra del Fuego (southern Argentina). An overview of recent progress. *Journal of Photochemistry and Photobiology B; Biology* 62: 67-77.

Pancotto V.A.; Sala S.E.; Cabello M.; López N.I.; Robson T.M.; Ballaré C.L.; Caldwell M.M.; Scopel A.L. (2003) Solar UV-B decreases decomposition in herbaceous plat litter in Tierra del Fuego, Argentina: Potential role of an altered decomposer community. *Global Change Biology* 9:1465-1474.

Pancotto V.A.; Sala O.E.; Robson T.M.; Ballaré C.L.; Caldwell M.M.; Scopel A.L. (2004) UV-B decreases leaf litter quality: effects on long term decomposition. *Submitted to Oecologia.*

Robson T.M.; Pancotto V.A.; Ballaré C.L.; Sala S.E.; Scopel A.L.; Caldwell M.M. (2003) Six years of solar UV-B manipulations affect growth of *Sphagnum* and vascular plants in a Tierra del Fuego peatland. *New Phytologist* 160: 379-389.

Robson T.M.; Pancotto V.A.; Ballaré C.L.; Sala S.E.; Scopel A.L.; Caldwell M.M. (2004) Reduction of solar UV-B mediates changes in the *Sphagnum* capitulum microenvironment and the peatland microfungal community. *Oecologia In Press.*

Robson T.M.; Pancotto V.A.; Scopel A.L.; Caldwell M.M. (2004) Solar UV-B influences microfaunal community composition in a Tierra del Fuego peatland. *Submitted to Global Change Biology.*

Manuscripts in Preparation

Robson T.M.; Pancotto V.A.; Ballaré C.L.; Sala S.E.; Scopel A.L.; Caldwell M.M. Response of three co-occurring *Nothofagus* species to solar UV-B manipulations.

Robson T.M.; Aphalo P.J. Effect of Ultraviolet-B radiation on the dynamics of leaf expansion in one year old *Betula pendula* and *B. pubescens*.

Posters presentations and conference proceedings

Aphalo P.J.; Robson T.M. Effects of ultraviolet-B radiation on the dynamics of leaf area expansion in birch (*Betula pendula* and *B. pubescens*), *at BES annual conference York, UK, 1998.*

Robson T.M.; Ballaré C.L.; Sala S.E.; Scopel A.L.; Caldwell M.M. Response of a Tierra del Fuego peatland to six field seasons of UV-B radiation manipulations, *at ESA annual conference, Tucson, Arizona, 2002.*

Robson T.M.; Ballaré C.L.; Sala S.E.; Scopel A.L.; Caldwell M.M. Biodiversity of microfaunal and fungal communities in a Sphagnum bog under two levels of solar UV-B, *at ESA annual conference, Madison, Wisconsin, 2001.*

Robson T.M.; Ballaré C.L.; Sala S.E.; Scopel A.L.; Caldwell M.M. Physiological and morphological responses of three *Nothofagus* species to UV-B radiation resulting

from Antarctic ozone depletion in Tierra del Fuego, southern South America, *at ESA annual conference, Snowbird, Utah, 2000.*

Robson T.M.; Zaller J.G.; Ballaré C.L.; Sala S.E.; Scopel A.L.; Caldwell M.M. The response of *Nothofagus* tree species to UV-B radiation resulting from ozone depletion, in the forests of Tierra del Fuego, *at SPARC 2000 Associated workshop on impacts of UV radiation on terrestrial and aquatic ecosystems. 9-11 Nov 2000, Mar del Plata, Argentina* (eds. Ballaré C.; Canziani P.O.; Helbing W.).

Robson T.M.; Ryel R.J. Rapid soil moisture recharge to depth by roots, *at Association of Applied Biologists conference Genotype-Phenotype Narrowing the Gaps, 16-18 December 2002, Cirencester, UK.*

Grants

Aphalo P.J.; Robson T.M.; Lehto T.; Kuitunen M. (2003) Does UV-B radiation affect allelopathy in European boral forests? The effects of fresh litter leacheates on seed germination and young seedlings. 22,000 Euros per year. *Submitted to the Maj & Tor Nessling foundation.*

Robson T.M.; Leffler A.J. (2003) Retrospective analysis of rhizome $\delta^{13}C$ isotope indicates historic growth conditions: Lepidochronology of *Tetroncium* rhizome and with $\delta^{13}C$ analysis. *Submitted to R. Ryel at the Ecology Center, Utah State University.*

Service

Journal referee; *Global Change Biology, Photochemical and Photobiological Sciences, Journal of Photochemistry and Photobiology B: Biology, Environmental and Experimental Botany, & Austral Ecology* (2003-2004).

Teaching and elucidation of biology and ecology; Ellis Elementary School, Logan Utah (2003); open day at CADIC, Tierra del Fuego (2000, 2001). Invited seminars at Fireland School in Ushuaia, Tierra del Fuego (2001, 2002), and Gloucestershire Wildlife Trust, UK (1998).

Guest lectures at Utah State University in Climate Change Ecology, Ecological Biophysics, Plant Physiological Ecology, and Wetland Management (Graduate Level Courses), Global Ecology (Undergraduate Course). Seminars for the Range Department, Biotechnology Center, IFEVA Buenos Aires (in Spanish), and CADIC, Tierra del Fuego (in Spanish).